

A NEW SUBFAMILY OF THE PTERASPIDIDAE (AGNATHA, HETEROSTRACI) FROM THE UPPER SILURIAN AND LOWER DEVONIAN OF ARCTIC CANADA

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ABSTRACT. New Pteraspidae from the upper Silurian and lower Devonian of arctic Canada differ from established members of the family in possessing a single orbito-cornual plate and a pineal plate enclosed by the dorsal disc. A new subfamily of the Pteraspidae, the Anchipteraspidinae, is raised to accommodate five species of the new genera *Anchipteraspis*, *Ulutitaspis*, and *Rhachiaspis*. Consideration of the growth and structure of the shields of the Anchipteraspidinae indicates their close relationship to both the Cyathaspidae and early members of the Pteraspidae. It is proposed that the Pteraspidae were developed from the Cyathaspidae by processes both of fusion and subdivision of the shield and that the Psammosteida developed from the Pteraspidae by similar processes.

LARGE numbers of heterostracans have been collected from Silurian and Devonian strata in the Yukon, British Columbia, and Northwest Territories and in recent years much of this material has been described (Denison 1963, 1964; Dineley 1964, 1968, 1976; Broad 1973; Broad and Dineley 1973; Dineley and Loeffler 1976; Loeffler and Jones 1976, 1977; Elliott 1983; Elliott and Dineley 1983). These descriptions have provided valuable information on the evolution of the Heterostraci, and indicate that the Canadian arctic was probably a centre of early development and radiation for this group. Evidence from these faunal descriptions indicates that anaspids, thelodonts, cyathaspids, and amphiaspids probably developed earlier there than elsewhere (Thorsteinsson 1967; Broad 1973), and more recent work (Elliott and Dineley 1983) has recorded the earliest known occurrence of *Protopteraspis* suggesting that pteraspidinids also evolved initially in this area. Further evidence for this view is provided in this work in which three new genera and five new species of heterostracans are described. These new genera are grouped as a new subfamily of the Pteraspidae and provide a link between that family and the Cyathaspidae, indicating an evolutionary connection.

The fauna is Upper Silurian and Lower Devonian in age and comes from the Peel Sound and Somerset Island Formations of Prince of Wales and Somerset Islands, Northwest Territories. Collections were made by the author in 1976 and by Bristol and Ottawa University parties in 1966, 1967, and 1974.

MATERIALS AND METHODS

The specimens described were preserved in slightly calcareous sandstones or calcareous siltstones. Both matrices allowed preparation by the transfer method of Toombs and Rixon (1950) in which the specimens were embedded in clear plastic and the matrix then removed with a dilute solution of acetic acid. This process enables the lateral line sensory canal system to be traced when the shields are viewed by transmitted light.

The measurements and ratios employed (Table 1) follow very closely those used by Denison (1964) when describing cyathaspids, except that the post-branchial length was not employed due to the difficulty of deciding the precise position of the branchial opening in pteraspids. The specimens are the property of the National Museum of Canada, Ottawa, and bear their catalogue numbers (prefixed NMC).

TABLE 1. Statistical comparison of dorsal shields of members of the Anchipteraspidinae. (Parameters selected for measurement are those used by Denison 1964.)

	Dimensions (mm)					Ratios			
	Med. length	Max. width	Orb. width	Orb. length	Pineal length	Max. width	Orb. width	Orb. length	Pineal length
						Med. length	Med. length	Med. length	Med. length
<i>Anchipteraspis crenulata</i>									
Range	26.0-28.5	20.0-23.0	9.5-10.5	3.0-3.5	4.5-5.0	0.78-0.81	0.35-0.39	0.11-0.14	0.15-0.19
Average	26.8	21.2	10.0	3.2	4.8	0.79	0.37	0.12	0.17
N=	4	4	4	4	4	4	4	4	4
<i>Ulutitaspis notidana</i>									
Range	32.5-35.0	22.0-23.0	12.0-13.5	4.0-5.5	6.5-7.5	0.63-0.71	0.34-0.40	0.12-0.15	0.19-0.21
Average	33.5	22.3	12.6	4.8	7.0	0.67	0.37	0.14	0.20
N=	4	6	6	6	5	4	4	4	4
<i>Ulutitaspis truncata</i>									
Range	20.0-21.5	18.5-19.0	9.5-10.5	3.0-4.0	4.5-6.5	0.93-0.97	0.45-0.53	0.15-0.20	0.23-0.32
Average	20.1	18.8	9.7	3.3	5.1	0.95	0.48	0.17	0.26
N=	4	4	4	4	4	4	4	4	4
<i>Ulutitaspis aquilonia</i>									
Range	25.5-29.0	21.5-24.0	11.5-13.0	3.0-4.5	4.0-6.5	0.80-0.84	0.42-0.45	0.11-0.15	0.19-0.22
Average	28.6	23.3	12.3	4.4	6.0	0.82	0.43	0.14	0.20
N=	4	4	4	4	4	4	4	4	4
<i>Rhachiaspis pteriga</i>									
Range	32.5-34.0	25.0-27.0	11.0-12.5	4.0-4.5	6.0-6.5	0.74-0.82	0.32-0.39	0.12-0.14	0.19-0.20
Average	32.6	25.6	11.6	4.1	6.2	0.78	0.35	0.13	0.19
N=	4	4	4	4	4	4	4	4	4

STRATIGRAPHY

The heterostracans described here were collected from the lower member of the Peel Sound Formation on Prince of Wales Island and the Somerset Island Formation on Somerset Island (text-fig. 1).

Rocks of the Peel Sound Formation occur over much of Prince of Wales Island and in gentle synclines in the Cape Anne-Pressure Point and Creswell Bay areas of Somerset Island. Originally named by Thorsteinsson and Tozer (*in Fortier et al.* 1963) the formation consists of red sandstones and siltstones, grading upwards into oligomict conglomerates and pebbly sandstones, deposited over a large delta system as subaerial alluvial fans prograding from the rising Boothia Uplift. On Prince of Wales Island, Miall (1970) separated the formation into lower and upper members. The lower, consisting of interbedded limestone, siltstone, sandstone, and oligomict conglomerate, is exposed only as a narrow band along the flank of the Boothia Uplift and has yielded large numbers of ostracoderms (Broad 1973; Broad and Dineley 1973; Loeffler and Dineley 1976; Elliott and Dineley 1983). The upper member is characterized by the disappearance of virtually all but conglomerate in the succession (Miall 1970). The Transition Bay localities on Prince of Wales Island all occur in the lower member of the Peel Sound Formation. This member is transitional between the marine Read Bay Formation and the upper member of the Peel Sound Formation.

On Somerset Island the localities occur in the Somerset Island Formation (Miall *et al.* 1978) which has been erected to include the transition beds between the Peel Sound sandstones and conglomerates and the underlying Read Bay limestones. It comprises a lower member consisting of grey and mottled planar-bedded limestones, and an upper member consisting of interbedded grey laminated dolostone and limestone, red quartzose siltstone, red dolosiltstone, and minor nodular limestone. The original

Read Bay–Peel Sound contact, defined (Thorsteinsson and Tozer 1963) at the occurrence of the oldest red siltstone unit, has been retained as the boundary between the two members of the Somerset Island Formation. The formation was deposited in predominantly intertidal and supratidal environments as the lowest part of a regressive sequence culminating in the conglomerate of the Peel Sound Formation. This unit is considered to be an age equivalent to the lower member of the Peel Sound Formation on Prince of Wales Island (Miall *et al.* 1978), both units representing the lowermost beds of a prograding clastic wedge, though separated by the Boothia Uplift and showing differences in lithology.

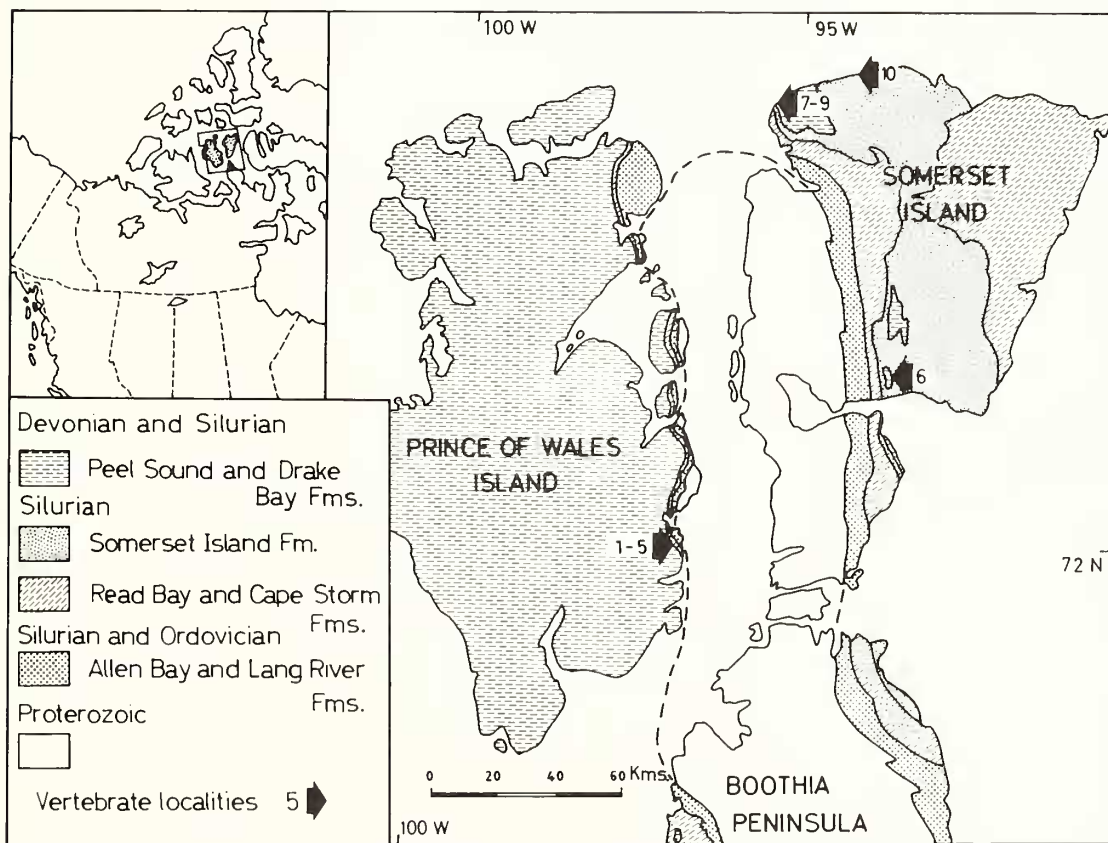
LOCALITIES

Prince of Wales Island

Locality 1. $96^{\circ} 32' \text{ W}$, $72^{\circ} 11' \text{ N}$. Gorge 26.4 km north of Transition Bay. 15 m above base of Peel Sound Formation. Grey, medium-grained sandstone grading up into poorly sorted conglomerate. Fauna: *Torpedaspis elongata*; *Corvaspis*; ?*Traquairaspis* sp.; cyathaspidids indet.; *Ulutiaspis notidana* gen. et sp. nov.

'Unnamed gorge' of Broad (1973); Broad and Dineley (1973). 22.5 km north of Transition Bay. $96^{\circ} 28' \text{ W}$, $72^{\circ} 10' \text{ N}$.

Locality 2. North side of gorge, 10.5 m above top of Read Bay Formation. Medium-grained grey sandstone with quartz clasts at base. Heterostracans concentrated at base where shields are stacked and current aligned.



TEXT-FIG. 1. Collecting localities and geology of Prince of Wales and Somerset Islands and Boothia Peninsula.

(Locality 7 of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10045.) Fauna: *Boothiaspis alata*; *B. angusta*; *B. ovata*; *Torpedaspis elongata*; *Poraspis* cf. *P. polaris*; *Corvaspis* sp.; ?*Traquairaspis* sp.; *Ulutitaspis truncata* gen. et sp. nov.

Locality 3. North side of gorge, 95.6 m above top of Read Bay Formation. 1 m thick medium to fine-grained sandstone, red at base and showing desiccation cracks. Fish occur throughout. (Locality 7 of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10046.) Fauna: *Torpedaspis elongata*; *Boothiaspis* sp.; *Corvaspis* sp.; ?*Traquairaspis* sp.; cyathaspidids indet.; acanthodian spines; *Ulutitaspis notidana* gen. et sp. nov.

Locality 4. North side of gorge. 60.3 m above top of Read Bay Formation (Broad, pers. comm. 1977). Probably equivalent to locality 3. 7 m of grey-green, fine-grained sandstone with dolomitic matrix. All ostracoderm material is black. Fauna: *Lingula* sp.; *Poraspis* cf. *P. polaris*; *Corvaspis* cf. *C. kingi*; ?*Traquairaspis* sp.; *Ulutitaspis* sp., gen. nov.

Locality 5. South side of gorge. 80.7 m above top of Read Bay Formation. 1.3 m of red medium-grained, finely laminated sandstone. Matrix dolomitic and calcareous. Fauna: *Corvaspis* cf. *C. kingi*; ?*Traquairaspis* sp.; *Ulutitaspis notidana* gen. et sp. nov. (*Listraspis* sp. in Broad (1973); Broad and Dineley (1973)).

Somerset Island

Locality 6. 93° 45' W. 72° 52' N. Kanguk Gorge, 8 km north of Creswell Bay. Upper member of Somerset Island Formation. Fauna: *Corvaspis* sp.; ?*Traquairaspis* sp.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 7. 95° 17' W. 73° 58' N. Cliffs on the north-east side of Pressure Point. Locality approximately 45 m below the top of the lower member of the Somerset Island Formation. (Locality 5 (part) of Broad (1973); Broad and Dineley (1973); G.S.C. locality C-10049.) Fauna: *Torpedaspis elongata*; *Boothiaspis ovata*; *Pionaspis acuticosta*; ?*Traquairaspis* sp.; Acanthodii indet.; *Ulutitaspis notidana* gen. et sp. nov.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 8. 95° 14' W. 73° 59' N. Stream valley 1.6 km east of Pressure Point. 15.2–31.4 m above the base of the upper member of the Somerset Island Formation (Gibling pers. comm. 1977). Grey, white, and buff, coarse to fine-grained, crossbedded sandstone. (Locality A of Dineley (1968); locality 5 (part) of Broad (1973), Broad and Dineley (1973); *Corvaspis* locality of Dineley and Loeffler (1976); G.S.C. locality C-10050.) Fauna: *Torpedaspis elongata*; *Boothiaspis alata*; *Corvaspis arctica*; *Hemicyclaspis murchisoni*; ?*Traquairaspis* sp.; Acanthodii indet.; *Ulutitaspis aquilonia* gen. et sp. nov.

Locality 9. 95° 14' W. 73° 57' N. Small bluff on the north-east side of the stream draining the north side of the cliff 4 km south-east of Pressure Point. Reported (Broad and Dineley 1973) as being 260' above the base of the Peel Sound Formation. Remapping by Miall (Miall and Kerr 1977) places this locality in member 1 or 2 of the redefined Peel Sound Formation. Slightly calcareous, white, crossbedded sandstone. (Locality 5 (part) of Broad (1973), Broad and Dineley (1973); G.S.C. locality C-10052.) Fauna: *Torpedaspis elongata*; *Corvaspis* sp.; *Pionaspis* sp.; ?*Traquairaspis* sp.; olbiaspid indet.; Cyathaspidids indet.; *Rhachiaspis pteriga* gen. et sp. nov.

Locality 10. 94° 09' W. 74° 08' N. Near sea level in small graben 8 km west of Cunningham Inlet. 21.3 m above the base of the upper member of the Somerset Island Formation. Blue, slightly calcareous sandstone. (Locality F of Fortier *et al.* (1963); locality 5 (part) of Broad (1973), Broad and Dineley (1973); G.S.C. locality C-10053.) Fauna: *Torpedaspis elongata*; *Corvaspis* sp.; *Pionaspis* sp.; ?*Traquairaspis* sp.; Acanthodii indet.; *Anchipteraspis crenulata* gen. et sp. nov.

SYSTEMATIC PALAEOLOGY

Order HETEROSTRACI Lankester 1868

Family PTERASPIDIDAE Claypole 1885

Diagnosis. (Amended after Denison 1970.) Heterostraci with dorsal shield composed of rostral and pineal plates, a dorsal disc with a dorsal spine attached to its posterior margin, and paired branchial, orbito-cornual, or orbital and cornual plates, the latter occasionally reduced or absent. Ventral shield formed by a large ventral disc, variably developed paired lateral, oral, and sometimes postoral plates, and in *Doryaspis* a pseudorostrum. Branchial openings more or less posteriorly placed at or near the lateral margin of the dorsal shield, typically at the posterior ends of the branchial plates and commonly bounded posteriorly by cornual plates. Sensory canals of dorsal disc arranged in two

longitudinal pairs connected on each side by three commissures, normally radially arranged. Ornamentation fine and commonly crenate. Scales small, numerous, and rhomboid.

Remarks. The family Pteraspidae was divided into two subfamilies by Denison (1970), the Doryaspidinae containing the aberrant pteraspidid *Doryaspis*, and the Pteraspinae containing all other forms. A further subfamily, the Anchipteraspinae, is established in this work to include forms that possess a single orbito-cornual plate and a pineal plate enclosed by the dorsal disc.

Subfamily ANCHIPTERASPIDINAE subfam. nov.

Diagnosis. Dorsal shield composed of rostral and pineal plates, a dorsal disc with posterior dorsal spine and paired branchial, dorsal, and orbito-cornual plates. Pineal plate totally enclosed by the dorsal disc. Branchial openings more or less posteriorly placed and bounded dorsally by the orbito-cornual plate. Narrow pre-oral surface ornamented by dentine ridges. Dorsal sensory canal system composed of paired lateral and medial longitudinal canals joined by three pairs of lateral commissures. Inter-orbital canal forming posteriorly directed loop on the dorsal disc, median longitudinal canals not contacting inter-orbital canal. Ventral shield formed by a large ventral disc.

Genera assigned. *Anchipteraspis* gen. nov., *Ulutitaspis* gen. nov., *Rhachiaspis* gen. nov.

Remarks. In the complement of plates the Anchipteraspinae shows most similarity to the Pteraspinae though in some features the relationship to the Cyathaspididae can still be clearly seen. The main points of difference are that the pineal plate in the Anchipteraspinae is still totally enclosed by the dorsal disc whereas that of the Pteraspinae is situated on the margin between the dorsal disc and the rostral plate; also the orbital and pineal plates of the Pteraspinae are represented by one plate, the orbito-cornual, in the Anchipteraspinae.

An enclosed orbit is characteristic of the Pteraspidae though this feature is also found in a number of cyathaspidids, notably in the Ctenaspidinae and in *Listraspis*. Denison (1964) has shown that in the cyathaspidid *Listraspis* this enclosure is due to the fusion of a sub-orbital plate to the dorsal shield. There is no clear evidence as to the method of enclosure of the orbit in the Anchipteraspinae though there is disruption to the ornamentation below the orbit in several specimens which may indicate fusion of a sub-orbital plate.

Fusion of the branchial plate to the dorsal shield is likewise a pteraspidid feature. In the Cyathaspididae the simple, notched plate is normally separate though in *Listraspis* a plate of typically cyathaspidid type is fused to the dorsal shield and in the Ctenaspidinae the branchial plate appears to have become incorporated in the dorsal shield as a lateral lamina and ventrolateral plate.

The pattern of the dorsal lateral line canals in the Anchipteraspinae is very close to that found in the primitive pteraspidid *Protopteraspis*, showing two pairs of longitudinal canals joined by three sets of commissures, a posterior loop of the inter-orbital canal, and no contact between the medial dorsal canals and the inter-orbital canal. No cyathaspidid shows as regular and complete a pattern.

The separate dorsal spine is not a cyathaspidid feature. Though spines are present in such forms as *Cyathaspis* and *Listraspis* there is no evidence that they are more than an outgrowth of the dorsal shield (Kiaer 1932; Denison 1964).

Classification within the Cyathaspididae and the Pteraspidae is based on characters derived almost entirely from the dorsal shield, and the most important of these is the mode of formation of the shield. In the Pteraspidae the plates comprising the dorsal shield were initiated at a juvenile stage, remained separate during the life of the animal while increasing in size by peripheral accretion, and fused only at maturity (White 1935, 1958, 1973; Heintz 1938; Denison 1973). In the Cyathaspididae the shield formed at maturity (Denison 1964) though in some forms the epitega functioned as separate units in the growth of the superficial layer (Dineley and Loeffler 1976). Evidence from a specimen of *Ulutitaspis aquilonia* gen. et sp. nov. (NMC 13844, Pl. 2, fig. 3; text-fig. 7B) shows that the animal continued growing after development of the dorsal disc had been initiated. This effectively separates the Anchipteraspinae from the Cyathaspididae and shows that their affinities lie with the Pteraspidae.

Genus *Anchipteraspis* gen. nov.

Type species. *A. crenulata* gen. et sp. nov.

Name. Greek 'anchi' meaning almost and *Pteraspis*, the type species of the subfamily Pteraspidae.

Diagnosis. Dorsal shield small and broad, and with a very blunt rostrum. Ornamentation of extremely fine ridges (17/mm) with well-developed alternating lateral projections at the base. Narrow orbito-cornual plates with smooth lateral margins indented at the level of the branchial openings. Inter-orbital canal forming posteriorly directed loop on dorsal disc.

Anchipteraspis crenulata gen. et sp. nov.

Plate 22, figs. 1-3; text-fig. 2

Name. Latin 'crenulata' meaning minutely crenate, referring to the ornament of very fine crenate ridges.

Type material. Holotype NMC 13854, dorsal shield; Plate 22, figs. 1, 3; from locality 10, Peel Sound Formation, Somerset Island.

Other material. NMC 13853, 13855, 13856, 13857, dorsal shields.

Diagnosis. As for genus, the type being the only species. For dimensions see Table 1.

Locality. 10.

Description. The rostrum is broad and very short with a rounded anterior margin. The dorsal surface is convex and a conspicuous groove separates it from the convexity of the dorsal disc (NMC 13854; Pl. 22, fig. 1). Laterally the plate margins form deep pre-orbital lobes (Pl. 22, fig. 3) bounding the ventral pre-oral surface. The posterior margin of the ventral pre-oral surface is slightly concave, no median lobe is developed. The surface is very narrow, only 0.75 mm wide, and is little more than a maxillary brim similar to that found in *Listraspis* (Denison 1964) and ornamented with fine transverse dentine ridges.

The dorsal disc is domed anteriorly with parallel lateral margins and an almost transverse posterior margin, slightly concave to either side of the median process. In NMC 13855 a median ridge is present anterior to the dorsal spine. The pineal plate is large and oval and ornamented with ridges parallel to the plate margins.

The dorsal spine is only seen in NMC 13855 where it is incomplete and distorted. Anteriorly the median ridge of the dorsal disc appears to merge with the spine through an area of short irregular ridges, a feature common in the subfamily. Laterally the plate junction is demarcated by a distinct groove. Only the base of the spine is preserved but the ridge pattern suggests that it would have been backswept.

The large orbits are laterally placed, and the orbito-cornual plates form laminae with smooth lateral margins that maintain a constant width of about 2 mm to a point just past the branchial openings where they are constricted (NMC 13854; Pl. 22, figs. 1, 3). Posteriorly the laminae flare out to form posterolateral points similar in shape to the cornual plates of Pteraspidae. The ornamentation is generally longitudinal and continuous on both dorsal and ventral surfaces indicating that this is one plate, but in the holotype the ornamentation is

EXPLANATION OF PLATE 22

Fig. 1. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13854. Dorsal view, $\times 3$.

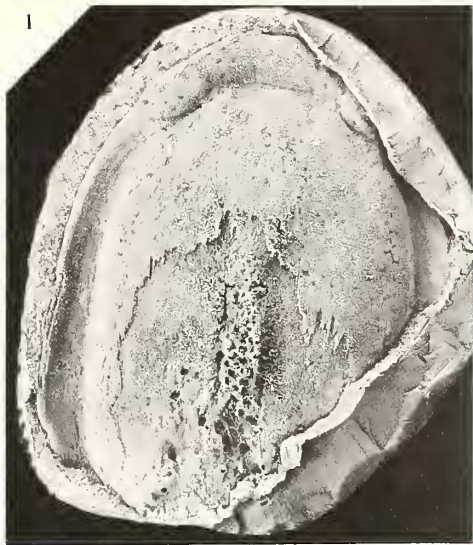
Fig. 2. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13853. Lateral view, showing branchial plate and branchial opening, $\times 3$.

Fig. 3. *Anchipteraspis crenulata* gen. et sp. nov. NMC 13854. Internal view of dorsal shield showing posterior part of orbito-cornual plate and impressions of internal organs, $\times 3$.

Fig. 4. *Ulutitaspis truncata* gen. et sp. nov. NMC 13835. Dorsal view, $\times 4$.

Fig. 5. *Ulutitaspis truncata* gen. et sp. nov. NMC 13836. Ventral pre-oral surface, $\times 10$.

Fig. 6. *Ulutitaspis truncata* gen. et sp. nov. NMC 13838. Dorsal view showing internal mould with impressions of internal organs, $\times 4$.



disrupted at the level of the branchial constriction suggesting the incipient development of separate cornual and orbital plates. Below the orbit the ornamentation is also disrupted and broken into short ridges (NMC 13854; Pl. 22, figs. 2; text-fig. 2A). This almost certainly indicates the final stage of enclosure of the orbit either by the fusion of a sub-orbital plate as occurs in *Listraspis* (Denison 1964), or by the growth of the orbital plates ventrolaterally around the orbits.

The branchial plate is attached dorsally to the medial edge of the ventral surface of the orbito-cornual plate, and is directed slightly medioventrally. The anterior end of the plate is blunt and the posterior margin, terminating at the base of the cornual extension of the orbito-cornual plate, is gently convex (Pl. 22, fig. 2; text-fig. 2A). The branchial opening is large and elongated and occurs about a third of the way from the posterior margin of the shield. The upper margin of the opening is damaged in NMC 13853 which shows it in lateral view, but in NMC 13854 it is clearly roofed by the ventral surface of the orbito-cornual plate.

A small plate is fused to the anterior margin of the branchial plate in NMC 13853 (Pl. 22, fig. 2; text-fig. 2A). A similar plate occurs in the same position in *Listraspis* (Denison 1964) and is certainly a lateral plate that has become fused to the dorsal shield.

The dorsal sensory canal system is visible only in NMC 13855 (text-fig. 2B). The pattern is very similar to that found in *Protopteraspis*, the most primitive genus of the subfamily Pteraspidae. Two pairs of longitudinal canals, medial and lateral, are joined by three pairs of transverse commissures. The medial canals terminate anteriorly before reaching the loop formed on the dorsal disc by the inter-orbital canal. The lateral canals join the inter-orbital canals behind the orbits before continuing ventrally.

No ventral shields are known for this genus.

Remarks. This genus is separated from *Rhachiaspis* gen. nov. by its smaller size and narrower orbito-cornual plates. It differs from *Ulutitaspis* gen. nov. chiefly in the smooth lateral margins present on the orbito-cornual plates.

The canal system shows considerable similarity to that found in *Protopteraspis* in having the same complement and arrangement of canals. However, it retains a certain rectangularity of arrangement that is closer to the pattern normally developed in the Cyathaspididae than to the radiating pattern found in the Pteraspidae.

Anchipteraspis is very similar in some aspects to the cyathaspidinid *Listraspis canadensis* (Denison 1964). The overall proportions are very similar as is the shape and relationships of the branchial plates. The orbito-cornual plate of *Anchipteraspis* is also very similar superficially to the laterally extended lateral epitegum of *Listraspis*. However, there is no separate pineal plate in *Listraspis* though a large pineal prominence is developed. There is also no indication of a posterior dorsal spine in *Listraspis*; a distinct postero-median process is developed but the ridges of the central epitegum curve into it showing that it is part of this epitegum and not a separate spine.

Genus *Ulutitaspis* gen. nov.

Type species. *U. notidana* gen. et sp. nov.

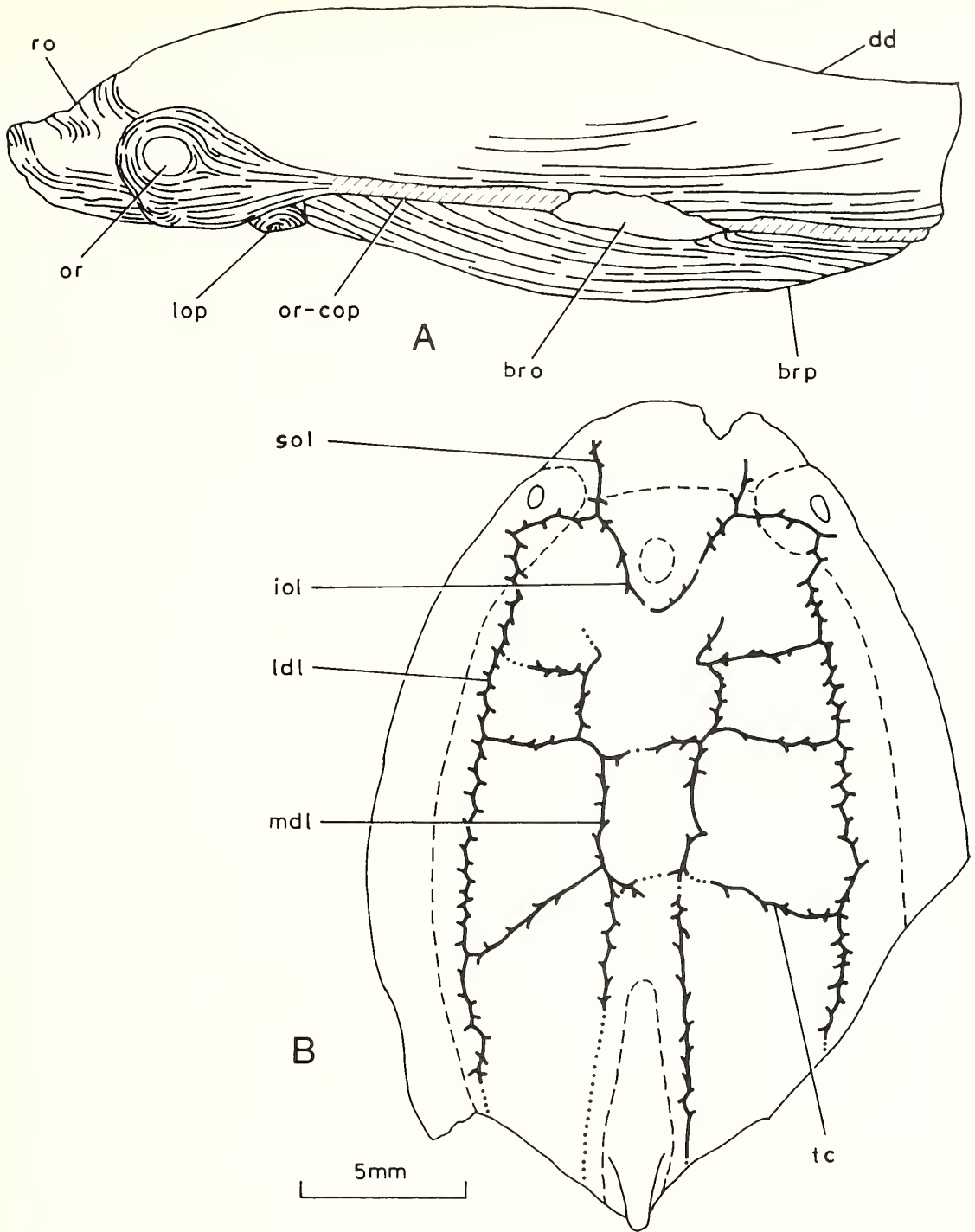
Name. Eskimo 'ulutit' meaning a saw, and Greek 'aspis' meaning shield referring to the serrated lateral margins of the dorsal shield.

Diagnosis. Dorsal shield small and gently arched, with generally high width ratio. Rostrum blunt, with well-developed median rostral process and broad ventral pre-oral surface ornamented with dentine ridges. Lateral margin of the orbito-cornual plate serrate for two-thirds of its length, the serrations increasing in size posteriorly. Cornual extension following deep notch at the level of the branchial opening. Well-developed, slender, posterior dorsal spine. Ornamentation of fine crenate ridges, becoming coarse and smoothly rounded at the lateral margins of the rostral and orbito-cornual plates.

Ulutitaspis notidana gen. et sp. nov.

Plate 23, figs. 1, 2; Plate 24, fig. 1; text-figs. 3, 4

Name. Greek 'notidanos' meaning with pointed dorsal fin, referring to the pointed dorsal spine.



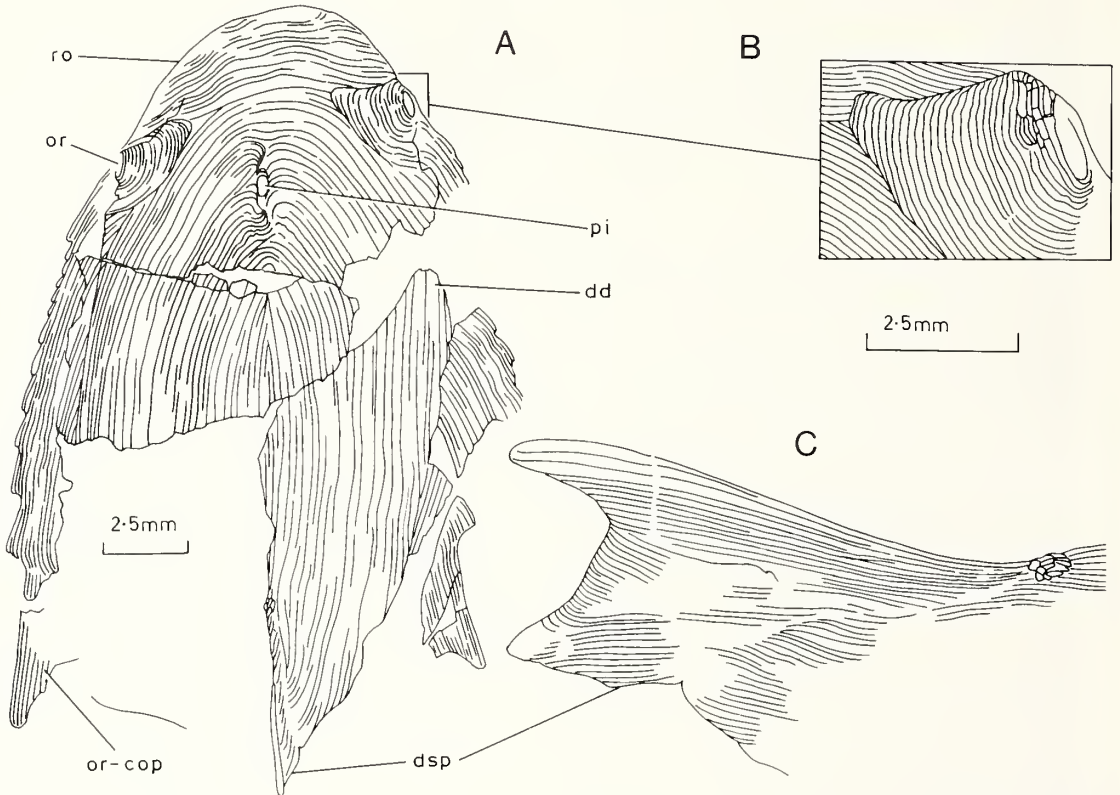
TEXT-FIG. 2. *Anchipteraspis crenulata* gen. et sp. nov. A, lateral view of dorsal shield, NMC 13853. B, dorsal sensory canal system, NMC 13855. Explanation of abbreviations for this and subsequent text-figs.: bro, branchial opening; brp, branchial plate; cep, central epitegum; cop, cornual plate; dd, dorsal disc; dsp, dorsal spine; gl, growth line; iol, interorbital canal; ldl, lateral dorsal canal; lep, lateral epitegum; lop, lateral oral plate; mdl, medial dorsal canal; mdr, median dorsal ridge; or, orbit; orp, orbital plate; or-cop, orbito-cornual plate; pa, pineal macula; pi, pineal plate; rep, rostral epitegum; ro, rostral plate; sol, supraorbital canal; sop, suborbital plate; tc, transverse commissure; vps, ventral pre-oral surface.

Type material. Holotype NMC 13823, dorsal shield; Plate 23, figs. 1, 2; from locality 3, lower member of the Peel Sound Formation, Prince of Wales Island.

Other material. NMC 13824–13832, 13834, dorsal shields; NMC 13833, ventral shield.

Diagnosis. Shield relatively slender (width ratio 0.63–0.71) with blunt almost transverse margin to rostrum. Dorsal spine slender and backswept. Small pineal plate. Straight lateral margin to cornual extension. Inter-orbital canal forming particularly deep narrow posteriorly directed loop on the dorsal disc. For dimensions see Table 1.

Localities. 1, 3, 5, 7.



TEXT-FIG. 3. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. A, dorsal view. B, detail of orbital area. C, dorsal spine in lateral view. For explanation of abbreviations see text-fig. 2.

EXPLANATION OF PLATE 23

Fig. 1. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. Internal mould of dorsal shield showing impressions of internal organs, $\times 3$.

Fig. 2. *Ulutitaspis notidana* gen. et sp. nov. NMC 13823. Dorsal view, $\times 3$.

Fig. 3. *Ulutitaspis aquilonia* gen. et sp. nov. NMC 13844. Dorsal view showing growth lines, $\times 4$.

Fig. 4. *Ulutitaspis aquilonia* gen. et sp. nov. NMC 13840. Dorsal view, $\times 4$.



ELLIOTT, *Ulutitaspis*

Description. *U. notidana* has a gently arched dorsal shield and is narrower than the other members of the genus, having a width ratio of only 0.67 on average. The ornamentation is of crenate ridges but these are coarser than in *Anchipteraspis crenulata*, averaging 11/mm on the dorsal disc, and decreasing to 7/mm on the lateral margin of the orbito-cornual plate where they become broad and rounded and lose the lateral projections at the base.

The rostral plate is short and broad and bears transverse dentine ridges. Posteriorly the ridges are parallel to the plate margin, anteriorly they break up into short ridges and denticles which extend on to a ventral laminae formed by the downturning of the anterior and lateral edges of the rostrum. This laminae forms a deep pre-orbital lobe and a shallow median lobe. Ventrally the pre-oral surface is ornamented with transverse dentine ridges, it is up to 2 mm deep and bears a slight posterior median projection (Pl. 24, fig. 1).

The broad elliptical ridge pattern of the dorsal disc is interrupted anteriorly by the small pineal plate. Centrally the ridges run almost longitudinally, meeting at a slight angle over a low median crest, variably developed before the dorsal spine.

The dorsal spine is long and gently sloping, its posterior point reaching a height of 4 mm above the dorsal shield in the holotype. The spine is ornamented with longitudinal dentine ridges, coarse and broadly rounded on the dorsal edge, fine and serrate on the lateral margin where they meet those of the dorsal disc at a sharp angle. Anteriorly there is an area of short irregular ridges spreading from the dorsal disc and obscuring the margin with the dorsal spine.

The orbito-cornual plates have oblique ridges meeting those of the dorsal disc at a slight angle. As in the other members of the subfamily there is an area of disrupted ornamentation below the orbit, indicating that the process of orbital enclosure has not yet reached the final stage seen in the Pteraspidae. Above the orbits the plates are expanded to form medial projections indicating development towards the pineal plate. The lateral laminae of the plates have a serrated margin, the serrations increasing in size posteriorly and in the holotype reaching a final depth of 1.5 mm and length of 2.5 mm (Pl. 23, fig. 1; text-fig. 3A). At the level of the branchial opening the laminae narrow abruptly and in some specimens a break in ornamentation is present at this point. The cornual part of the plate has a straight lateral margin and a rounded point projecting past the posterior margin of the shield.

The branchial plate is known only from two partial specimens. In NMC 13826 the internal aspect of the opening can be seen, showing it to have an abrupt, vertical anterior margin and a chamber that is triangular in cross-section. The branchial plate is fused to the ventral surface of the orbito-cornual plate which also roofs the branchial opening.

The dorsal sensory canal system is well preserved in the holotype and in NMC 13830 (text-fig. 4). It follows the pattern normal for the subfamily, though the loop formed on the dorsal disc by the inter-orbital canal is very narrow and extends further back than in any other species. In the holotype the lateral longitudinal canals are well within the lateral margins of the dorsal disc. In NMC 13830 the lateral canals are close to the plate margins but the similar areal extent of the canal systems in the two specimens suggests that further growth has taken place in the holotype after enclosure of the canals.

The one ventral shield is an internal cast and shows nothing of the dentine ridge pattern or the canal system. The shield is gently arched and has a blunt anterior border with a slight median concavity and a strongly convex posterior border.

Remarks. *U. notidana* is separated from *U. truncata* and *U. aquilonia* by its larger size and more slender form. *Rhachiaspis pteriga* is similar in size but possesses broader orbito-cornual plates with smooth lateral margins, and a vertical dorsal spine. *A. crenulata* is smaller, lacks a serrated margin to the orbito-cornual plate, and has a more curved lateral margin to the cornual extension.

Ulutitaspis truncata gen. et sp. nov.

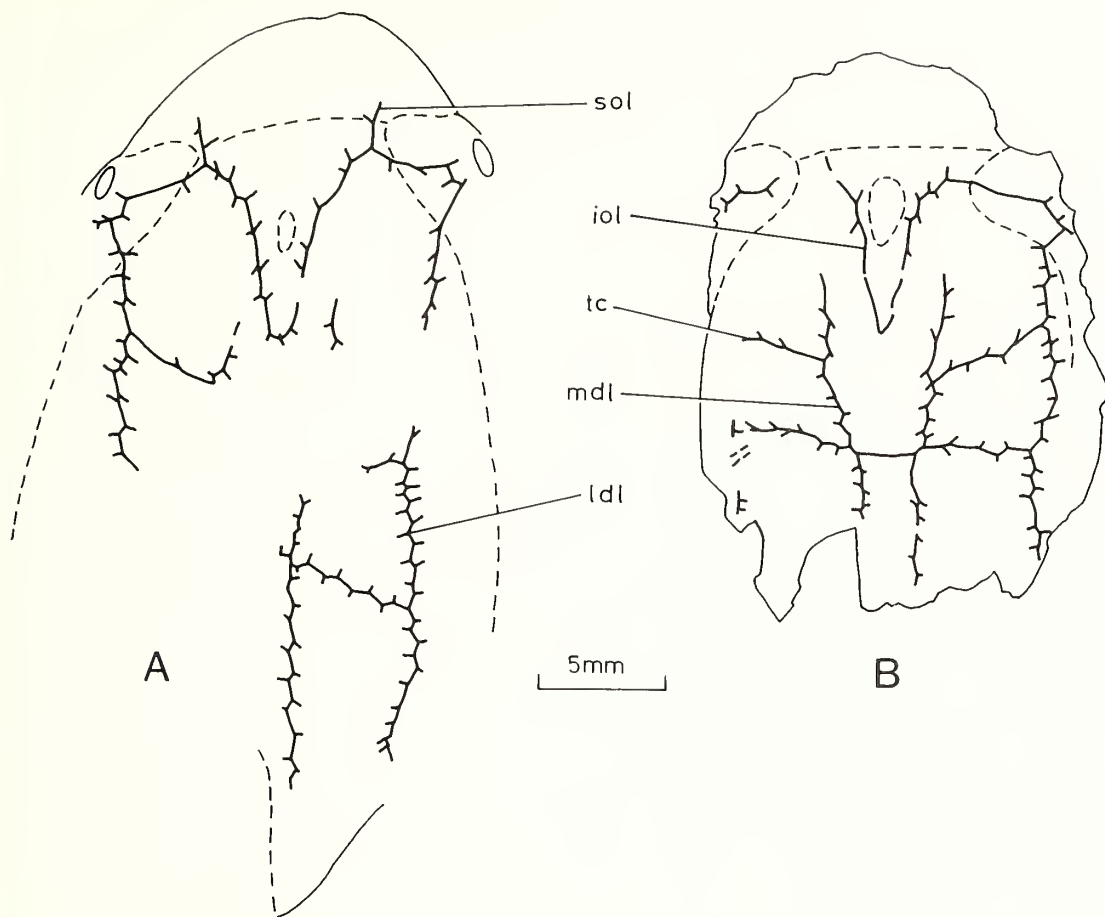
Plate 22, figs. 4–6; text-fig. 5

Name. Latin 'truncare' meaning to shorten, referring to the shortness of the dorsal shield.

Type material. Holotype NMC 13835, dorsal shield; Plate 22, fig. 4; from locality 2, lower member of the Peel Sound Formation, Prince of Wales Island.

Other material. NMC 13836–13839, dorsal shields.

Diagnosis. Dorsal shield small, strongly arched, and with a very high width ratio (0.93–0.97). Dentine ridges on rostrum curve round two centres on the anterior margin. Well-developed ventral pre-oral surface. For dimensions see Table 1.



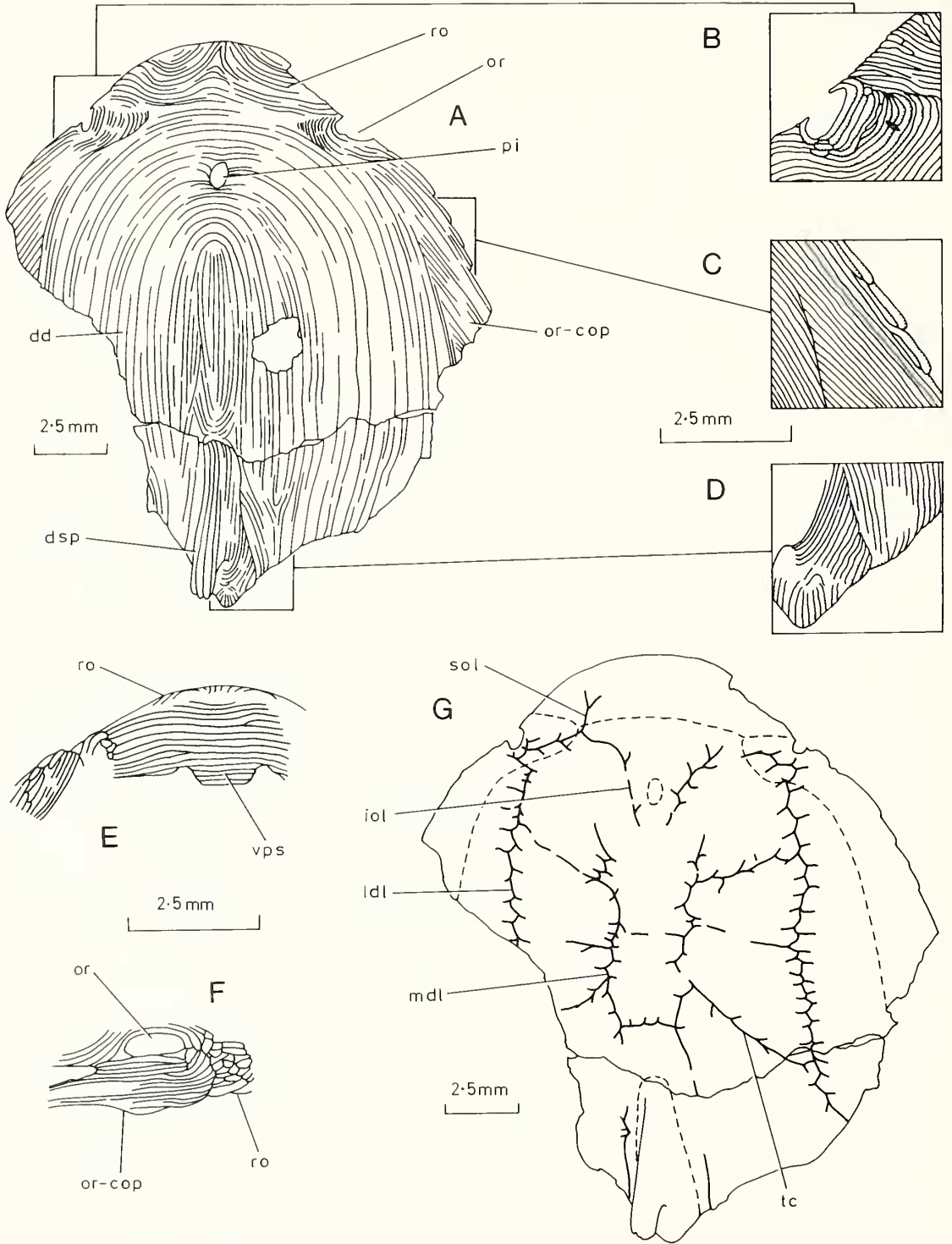
TEXT-FIG. 4. *Ulutitaspis notidana* gen. et sp. nov. Dorsal sensory canal system. A, NMC 13823. B, NMC 13830. For explanation of abbreviations see text-fig. 2.

Locality. 2.

Description. This is an extremely broad form with a width ratio greater than any other member of the Pteraspidae and rivalled only by *Ctenaspis* and *Listraspis* among the Cyathaspidae.

The broad rostrum has a rounded anterior margin and the dentine ridges curve around two anterolateral centres so that medially the ornamentation is longitudinal (Pl. 22, fig. 4; text-fig. 5A). The ridges coarsen in this area to 7/mm from 15/mm on the posterior margin of the plate, and also break up into short ridges and denticles running on to the ventral lamina. The ventral pre-oral surface is deeper and broader in this species than in the other members of the genus. In the holotype it is 2 mm deep and ornamented with transverse dentine ridges averaging 9/mm (Pl. 22, fig. 5; text-fig. 5E).

The dorsal spine is present in the holotype where it is slender and slopes back at a shallow angle, reaching 3 mm above the dorsal shield though the tip is broken. Laterally the ridges of the spine meet those of the dorsal disc at a sharp angle and a shallow sulcus is formed at the plate junction. Anteriorly the plate boundary is indistinct owing to the presence of an area of short irregular ridges. On the posterior point of the median process in the holotype two small scale-like areas are delineated by the ornamentation (text-fig. 5D). These probably indicate the presence of small scales absorbed into the posterior margin of the shield.



TEXT-FIG. 5. *Ulutitaspis truncata* gen. et sp. nov. A, dorsal view; B, C, D, details of orbit, orbito-cornual plate and dorsal spine; NMC 13835. E, ventral pre-oral surface; F, detail of orbit; NMC 13836. G, dorsal sensory canal system, NMC 13835. For explanation of abbreviations see text-fig. 2.

The orbito-cornual plates are similar to those found in the other members of the genus, differing only in their greater width. The posterior point is blunt and the outline of the cornual part of the plate is similar to that of *U. notidana*. In this species the ornamentation below the orbit is not broken into short lengths as is the case in the type species and in *Anchipteraspis crenulata*. This may indicate that in this species the process of orbital enclosure has been completed.

The branchial plate is generally similar to that of *A. crenulata* though there is no fused lateral plate on the anterior termination. The branchial opening is set well back under the cornual part of the orbito-cornual plate and is posteriorly directed.

The dorsal sensory canal system is similar to that found in the other members of the genus (text-fig. 5G). The only difference lies in the proportions, due to the shortness of the shield in *U. truncata*.

There are no specimens of the ventral shield.

Remarks. The presence of orbito-cornual plates with serrated lateral margins confine this species to the genus *Ulutitaspis*. It is distinguished from the other members of the genus by its small size, very high width ratio, and details of rostral ornamentation.

The change in ornamentation on the posterior point of the posterior median process in the holotype probably indicates the attachment of small scales, a feature that is not infrequently found on the posterior margin of dorsal shields in the Pteraspidae. It has been suggested by Denison (1960, 1964) that the dorsal spine in the Pteraspidae originated by this process. A large median dorsal scale becoming incorporated into the dorsal disc and subsequently developing to form a spine whilst maintaining its status as a separate plate. The Anchipteraspidinae provide no information to support this view, rather they indicate that the dorsal spine originated as an outgrowth of the dorsal shield that subsequently developed as a growth centre and became a separate plate.

Ulutitaspis aquilonia gen. et sp. nov.

Plate 23, figs. 3, 4; text-figs. 6, 7

Name. Latin 'aquilonaris' meaning north and referring to the area in which it was discovered.

Type material. Holotype NMC 13840; Plate 23, fig. 4; from locality 2, upper member of the Somerset Island Formation, Somerset Island.

Other material. NMC 13841–13844, dorsal shields.

Diagnosis. Dorsal shield oval in outline and gently arched, between 25.5 and 29.0 mm long and with a width ratio of 0.80 to 0.84. Rostrum short and rounded, posterior extension of the orbito-cornual plate long and curved. For dimensions see Table 1.

Locality. 8.

Description. The specimens of this species are generally poorly preserved. In the holotype (Pl. 23, fig. 4; text-fig. 6A) the posterior median process is missing and the length has been estimated with information from NMC 13844.

The rostrum is broad and rounded, with transverse ornamentation. There is a broad ventral pre-oral surface, ornamented with transverse dentine ridges and up to 2.5 mm deep in the centre where the posterior margin bears a low median lobe.

The pineal plate is larger than in the other members of the genus and in the holotype is ornamented with short longitudinal ridges. The longitudinal ornamentation in the midline of the dorsal disc breaks up into an area of short ridges in front of the dorsal spine, but in NMC 13844 (Pl. 23, fig. 3; text-fig. 7A) the dorsal disc is marked by growth lines, indicated by irregularities in ridge pattern. Two almost complete growth lines can be traced and the first of these shows an anterior notch for the pineal body. The later growth line curves round the margin of the pineal plate, however, and between the pineal plate and the notch in the first growth line is an area of short irregular ridges. This appears to show that the organism increased in size between the development of the two growth lines as the pineal organ clearly moved forward in that time. The dorsal spine is known from two specimens (NMC 13840 and 13844, text-fig. 7C) both incomplete. The shape, however, appears to be very similar to that in the other members of the genus.

The orbito-cornual plates are incomplete in the holotype but they are sufficiently well preserved to show the lateral serrations. The posterior termination to the plate is preserved in NMC 13841 (text-fig. 6C) which shows it to be a sharply pointed projection with a convex outer margin and straight inner margin. This contrasts with the shorter blunt terminations to the plate in *U. notidana* and *U. truncata*.

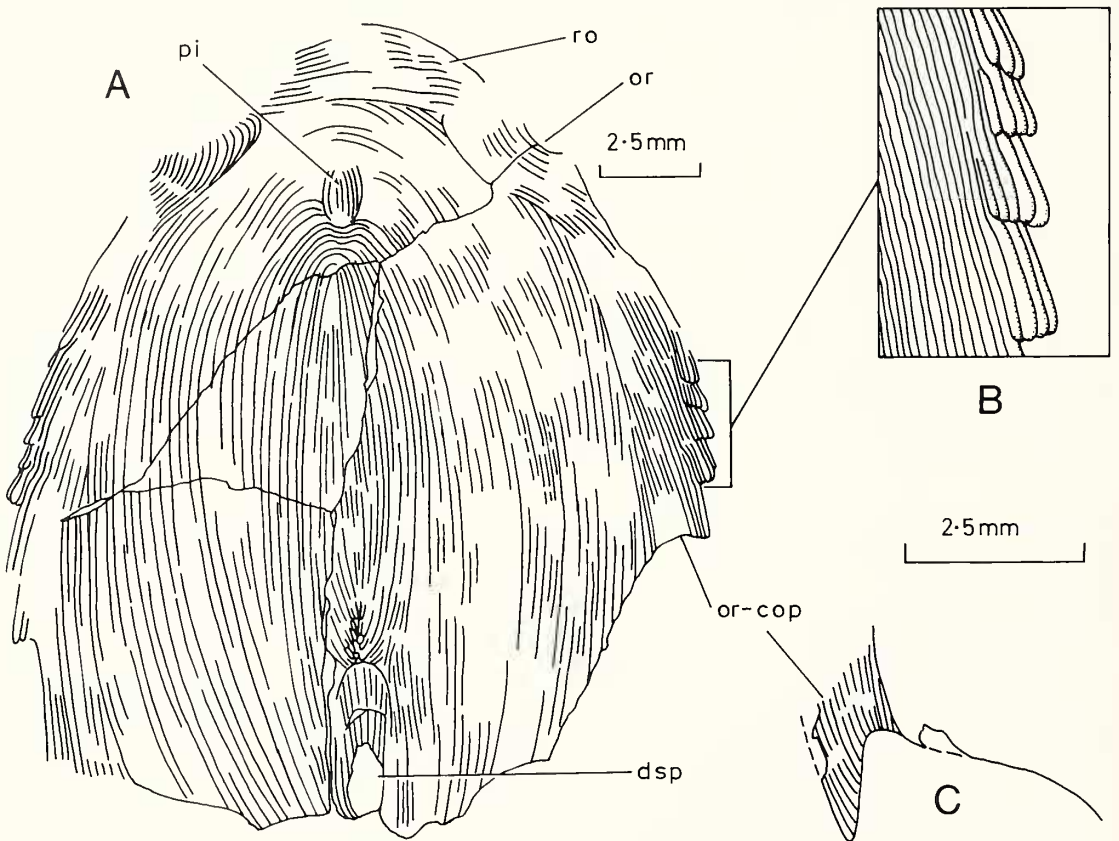
The branchial plate is known only in internal view (NMC 13841) and is relatively short with a large branchial opening.

The dorsal sensory canal system is essentially the same as that found in the other members of the genus (text-fig. 7A).

There are no specimens of the ventral shield.

Remarks. This species is separated from the others in the genus by the width ratio of the dorsal shield, which lies between that of the other two species, and by the slender, pointed posterior terminations to the orbito-cornual plates which differ from the short blunt terminations found in the other forms.

The evidence provided by the growth lines on the dorsal disc of NMC 13844 is of the greatest importance. These lines record the mode of growth of the shield and not only show that the dorsal disc was initiated at a median growth centre and developed by peripheral accretion but also that the animal continued growing during the early stages of this process. This is indicated by the fact that though the first growth line shows a notch for the pineal plate the final position of the plate is further forward showing an increase in size of the organism between the formation of the two growth lines.



TEXT-FIG. 6. *Uluitaspis aquilonia* gen. et sp. nov. A, dorsal view; B, detail of lateral serrations; NMC 13840. C, posterior termination of left orbito-cornual plate, NMC 13841. For explanation of abbreviations see text-fig. 2.

This mode of growth of the shield is unlike that in the Cythaspidinae, in which growth of the animal had ceased when the shield started forming, and more like that found in the Pteraspida, where the plates were initiated at an early stage in the growth of the animal and remained separate, though increasing in size by peripheral accretion, until the adult stage was reached.

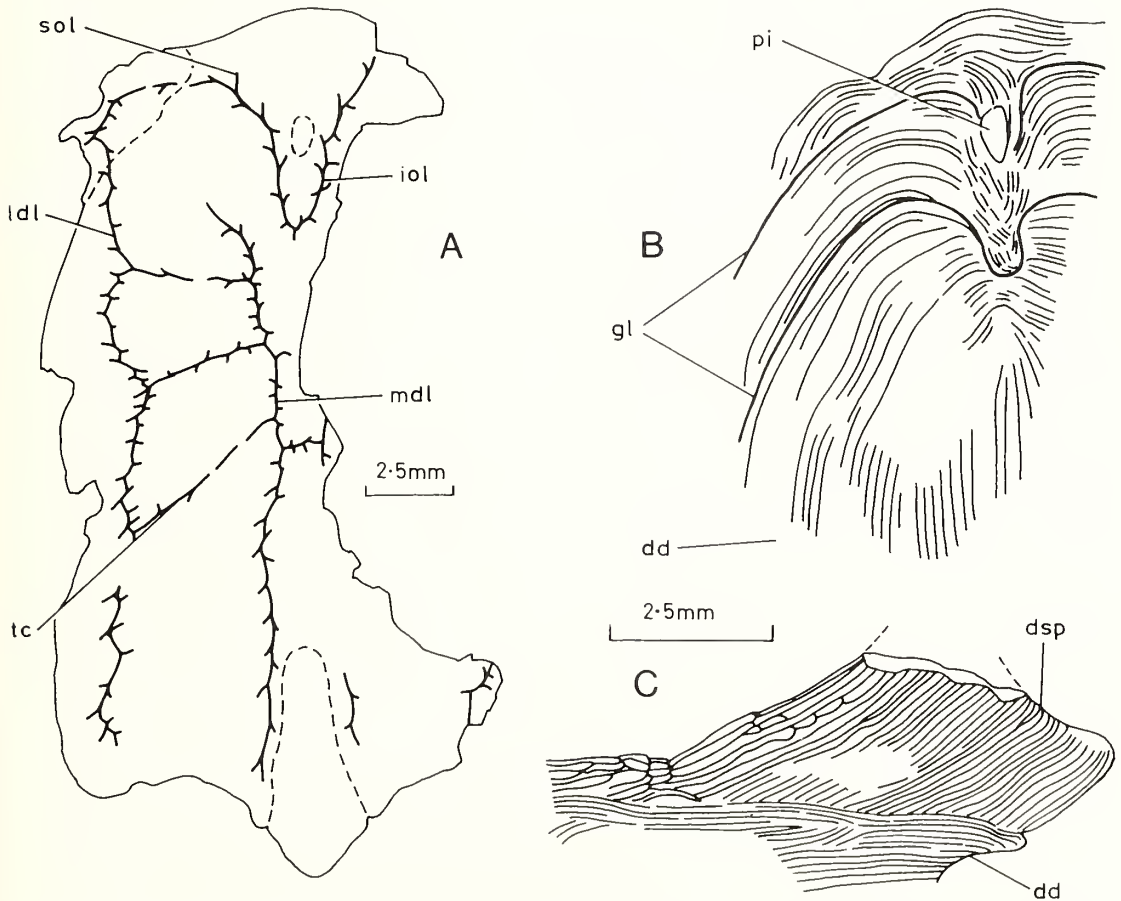
Ulutitaspis sp. indet.

Plate 24, fig. 2

Material. NMC 13846, dorsal shield.

Locality. 4.

Description. The dorsal shield is estimated to have been about 26 mm long and 17 mm wide. It is crushed and the posterior and left side are missing. The ornamentation is in all respects similar to that found in *Ulutitaspis* and the plate margins can be clearly seen. The anterior part of the orbito-cornual plate is present on the right side and the margin is serrated. The posterior part of the plate is missing, however, as is the dorsal spine. The bone is black and opaque and hence it is not possible to see any details of the dorsal sensory canal system.



TEXT-FIG. 7. *Ulutitaspis aquilonia* gen. et sp. nov. A, dorsal sensory canal system; B, detail of growth lines on dorsal shield; C, dorsal spine; NMC 13844. For explanation of abbreviations see text-fig. 2.

Remarks. This specimen shows enough of the features of the genus to be attributed to *Ulutitaspis*. It occurs at a locality within the stratigraphic range of *U. notidana* and most resembles that species, its width ratio of 0.65 and orbital width ratio of 0.38 falling within the size range for that form. It is very much smaller than any of the specimens of *U. notidana*, however, with a length of 26 mm and width of 17 mm compared with an average of 33.5 mm and 22.3 mm for *U. notidana*. As the specimen is incomplete no definite relationship can be determined and it is therefore referred merely to *Ulutitaspis* sp.

Genus *Rhachiaspis* gen. nov.

Type species. *R. pteriga* gen. et sp. nov.

Name. Greek 'rhachis' meaning backbone or ridge and 'aspis' meaning shield, referring to the prominent median dorsal ridge.

Diagnosis. Dorsal shield large and strongly vaulted, dorsal disc elongated and bearing a sharp median dorsal crest. Posterior margin deeply excavated between the median process and a pair of lateral processes. Spinal element waisted, the anterior part occupied by a spine with a vertical anterior margin, the posterior part with a median groove. Narrow ventral pre-oral surface with ornament of transverse dentine ridges. Orbito-cornual plates broad, upswept anteriorly and with broad curved cornual extensions.

Rhachiaspis pteriga gen. et sp. nov.

Plate 24, figs. 3-6; text-fig. 8

Name. Greek 'pteron' meaning wing and 'megas' meaning large, referring to the very broad orbito-cornual plates.

Type material. Holotype NMC 13851, dorsal shield; plate 24, figs. 4-6; from locality 7, lower member of Somerset Island Formation, Somerset Island.

Other material. NMC 13847, 13848, 13850, dorsal shields; NMC 13849, 13852, ventral shields.

Diagnosis. As for genus, the type being the only species. For dimensions see Table 1.

Localities. 6, 7, 9.

Description. The dorsal shield is large and broad with a short rostral plate. The ventral pre-oral surface forms a narrow band only 1 mm deep, ornamented with transverse dentine ridges and with a slight median lobe on the posterior margin.

The dorsal disc is elongated, rounded anteriorly, and almost parallel sided. It bears a conspicuous median crest extending from the centre of growth to the dorsal spine. In NMC 13847 this crest is extremely narrow and vertical and appears to merge with the dorsal spine, though in the holotype they are clearly separate. The posterior margin of the disc is very deeply excavated between the well-developed posterior median process and a pair of smaller posterolateral processes. The pineal plate is small and cannot be clearly seen in any specimen. In the holotype it interrupts the anterior ridge pattern of the dorsal disc and appears to be ornamented with short longitudinal ridges.

EXPLANATION OF PLATE 24

Fig. 1. *Ulutitaspis notidana* gen. et sp. nov. NMC 13828. Dorsal shield in internal view, $\times 2.5$.

Fig. 2. *Ulutitaspis* sp. gen. nov. NMC 13846. Dorsal view, $\times 3$.

Fig. 3. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13849. Ventral shield, $\times 3$.

Fig. 4. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal shield in lateral view, $\times 3$.

Fig. 5. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal view, $\times 3$.

Fig. 6. *Rhachiaspis pteriga* gen. et sp. nov. NMC 13851. Dorsal view of internal mould showing impressions of internal organs, $\times 3$.



The spine is characteristic in this genus. The base is divided into anterior and posterior parts by a median constriction, the anterior part bearing the dorsal spine which has an almost vertical leading edge and slopes posteriorly (Pl. 24, fig. 4). The spine is broken in the holotype and neither its total height nor the shape of its termination are known. Posteriorly the plate expands to the margin of the shield and in the holotype has a median sulcus ornamented with longitudinal ridges, separating a pair of lateral prominences ornamented with transverse ridges. This feature can only be seen in the holotype, where the surface detail is poor, but may indicate the presence of fused dorsal ridge scales.

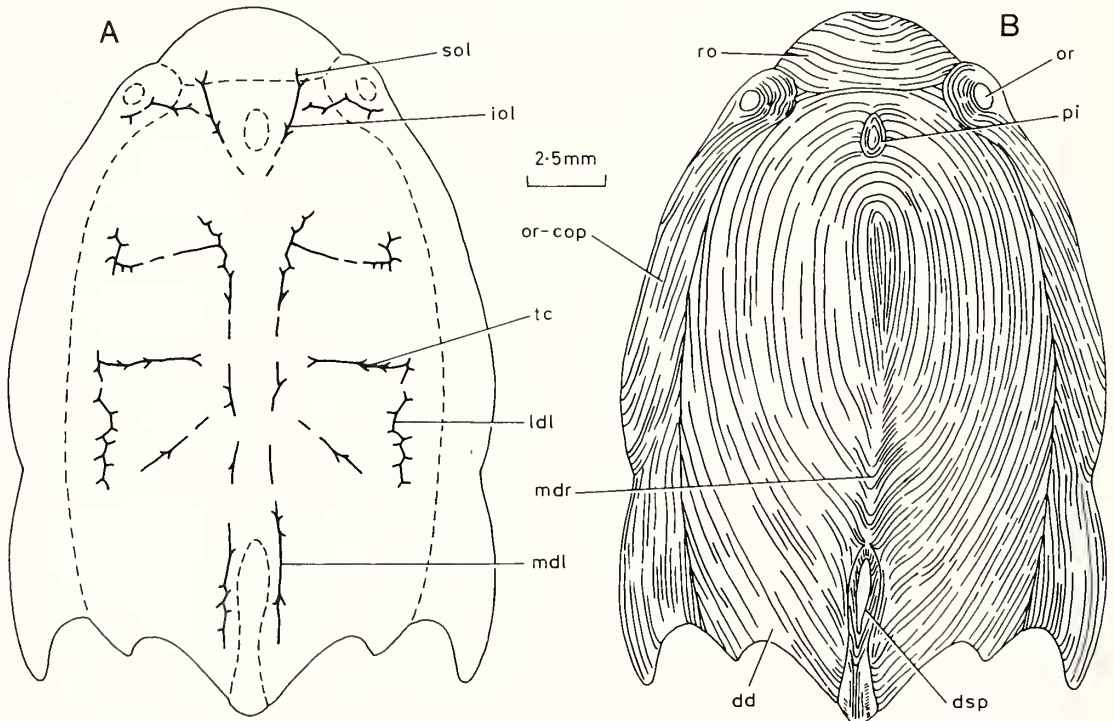
The orbits are prominent and laterally directed and there is no disruption of ornamentation below them. The lateral laminae of the orbito-cornual plates are very broad, and are very much upswept just behind the orbits. This feature can be seen in all the specimens and is not a distortion produced during preservation, it results in a concave dorsal surface to the plate anteriorly which fades away towards the middle of the plate.

The branchial plate is known only from internal casts and is similar to those found in other members of the subfamily.

The dorsal sensory canal system is not well preserved and it has been reconstructed (text-fig. 8A) based on NMC 13847 and 13851. It appears to show a pattern similar to that found in other members of the Anchipteraspidinae, though it is not possible to see if a complete loop is formed by the inter-orbital canal, nor if the median dorsal canals terminate before meeting the inter-orbital canal.

Of the two ventral shields known NMC 13849 is the best preserved (Pl. 24, fig. 3), and shows the ventral dentine ridge pattern and sensory canal system. Its shape is very similar to that found in the Pteraspida, with anteriorly a median depression, probably the site of attachment for sub-oral and oral plates, and posteriorly a slight median process. The generally elliptical ornament is interrupted anteromedially, the longitudinal median ridges meeting the transverse anterior ridges in an area of swirls and whorls.

The canal system is incomplete but appears to follow the pteraspid pattern with an anterior median loop and paired lateral canals giving rise to a number of lateral transverse commissures.



TEXT-FIG. 8. *Rhachiaspis pteriga* gen. et sp. nov. A, dorsal sensory canal system (based on NMC 13847 and 13851). B, reconstruction of dorsal shield. For explanation of abbreviations see text-fig. 2.

Remarks. This distinctive form is separated from the other members of the Anchipteraspidinae by its large size, broad upswept orbito-cornual plates, and vertical dorsal spine.

The keel-like median dorsal ridge, merging with the vertical dorsal spine, and the broad orbito-cornual plates are probably developments to aid the stability of the animal in swimming, as are the greatly extended cornual plates and tall dorsal spines developed in some pteraspids. The upswept anterior to the orbito-cornual plates would also have helped to give uplift to the anterior part of the body by increasing the area of the anterior bearing surface. These developments suggest that *R. pteriga* was an active and capable swimmer.

The waisted shape of the spine base is unknown elsewhere in the Pteraspidae. The posterior part of the plate is unfortunately not clear in the only specimen that shows it; it may represent included dorsal ridge scales as are present in the type specimen of *Uluittaspis truncata*.

AGE OF THE FAUNA

The Somerset Island localities occur almost exclusively within the Somerset Island Formation. Localities at West Creswell Bay and Cape Anne have been dated as early Pridolian (Miall *et al.* 1978) based on conodont faunas including *Ozarkodina confluens* and *Pelekysgnathus* sp. The base of the formation becomes younger eastwards across northern Somerset Island (Jones and Dixon 1977) and in the north-east part of the island the underlying Read Bay Formation is Pridolian. A fauna including *O. confluens* has been reported from the Leopold Formation in this area (Loeffler and Jones 1976, 1977) in association with ostracodes and ostracoderms, and dated (Uyeno *in* Loeffler and Jones 1977) as late Ludlow or early Pridolian. Thorsteinsson (1980) considers that the basal beds of the Somerset Island Formation on Boothia Peninsula are latest Ludlovian in age, on the basis of the presence of *Pedavis* sp. aff. *P. thorsteinssoni* (Uyeno 1980). The cyathaspidid *Torpedaspis elongata* occurs with this conodont on Boothia Peninsula and also occurs in the lower part of the Somerset Island Formation in north-western Somerset Island indicating a similar age there.

A number of the vertebrates provide independent evidence of age. *Boothiaspis alata* occurs in both members of the Somerset Island Formation at Pressure Point and also in the lower member of the Peel Sound Formation at Transition Bay. It also occurs in the Devon Island Formation on Ellesmere Island where it is associated with a monograptid dated as Pridolian by Thorsteinsson on Cornwallis Island (Broad 1973). *Ariaspis ornata* is known from the lower member of the Somerset Island Formation at Pressure Point but it has also been reported from Beaver River (Denison 1963) and the Delorme Formation (Dineley and Loeffler 1976). Though originally assigned an early or middle Ludlovian age on the basis of associated invertebrates, the age could range from Wenlockian to Pridolian (Dineley and Loeffler 1976) as *Monograptus dubius* which occurs above the Beaver River fauna is now known to extend from the Llandoveryan to the Pridolian (Broad and Lenz 1972).

Hemicyclaspis murchisoni, which occurs in the upper member of the Somerset Island Formation at Pressure Point, is regarded as an index fossil for the lowest Downtonian of Britain (White 1950), now considered to be equivalent to the early Pridolian (Loeffler and Dineley 1976). It therefore appears that the whole of the Somerset Island Formation is latest Ludlovian or Pridolian in age.

On Prince of Wales Island only the Transition Bay localities can be dated and correlated with those on Somerset Island. Invertebrate dating of the sequence through the lower member of the Peel Sound Formation has yielded upper Silurian ages (Bolton and Copeland *in* Broad and Dineley 1973; Bolton, pers. comm. 1976) for the whole of the sequence. Thorsteinsson (1980) concludes that the age range of the lower member of the Peel Sound Formation on Prince of Wales Island is late Ludlovian to early Pridolian, based mainly on the presence of *Hemiarges bigener* towards the top of the lower member. This trilobite is found at widely separated localities within the arctic archipelago, but wherever it can be related to diagnostic fossils it appears to be confined to beds of Pridolian age (Thorsteinsson 1980). Miall *et al.* (1978) consider the lower member of the Peel Sound Formation on Prince of Wales Island to be equivalent in age to the Somerset Island Formation though the rock types differ.

GROWTH AND DEVELOPMENT OF THE DERMAL SHIELD

The lack of a universally agreed interpretation of the mode of growth of the heterostracan shield has resulted in the development of many divergent views on the evolution of the order. The Anchipteraspidae show several features that are of value in illustrating the growth of the heterostracan shield and the evolutionary relationships between the heterostracan families. They show superficial similarity to both the Cyathaspididae and the Pteraspidae; however, both these groups have been shown to possess dissimilar modes of growth.

Growth of the Cyathaspididae. The cyathaspidid dorsal shield is divided into rostral, lateral, and central areas termed 'epitega' (Stensiö 1958), delineated by dermal ridge patterns and originally thought to be merely superficial divisions (Kiaer 1932; White 1935). The view that in some genera at least the epitega were distinct plates (Kiaer and Heintz 1935; Moy-Thomas 1939; Obrucsev 1945; Stensiö 1958) was supported by Denison (1964), who showed that the superficial layers developed first, possibly in separate epitegal units, and that the subsequent formation of the deeper layers may have occurred as one unit. It has now been demonstrated (Dineley and Loeffler 1976) that in some cyathaspidids the superficial layer not only grew independently in the epitegal areas but that growth took place incrementally. In *Pionaspis amplissima* (text-fig. 9A) successive growth lines indicate that formation of the shield did not start until the individual reached full size, and then continued by peripheral accretion from centres within each epitegum until the edges met and fused.

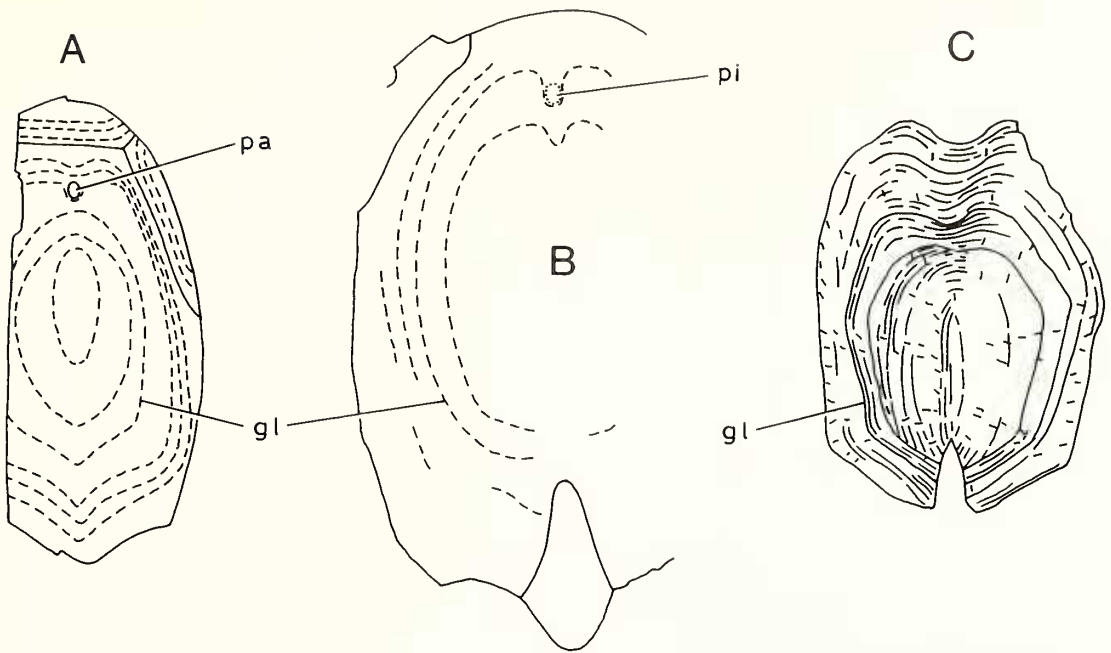
Growth in the Pteraspidae. Though it was originally thought (Zych 1931; White 1935) that development of the pteraspidae shield was not initiated until the individual had reached almost full size, as in the cyathaspidids, study of growth stages (Heintz 1938; White 1958) has demonstrated that after an early unarmoured stage the plates developed separately though remaining in contact peripherally (text-fig. 9C). Growth of the shield appears to have been initiated at a total length of about 23 mm (Denison 1973; White 1973), and ultimate fusion of the plates was delayed for a progressively longer period of time as the family evolved (White 1958). Evidence from thin sections shows that, as in the cyathaspidids, growth of the superficial layer preceded that of the cancellous and basal layers (Denison 1973; White 1973).

Growth in the Anchipteraspidae. In the Anchipteraspidae growth lines are visible on a number of specimens but only on one are they complete enough to throw any light on the process of growth in the subfamily. A specimen of *Ulutitaspis aquilonia* (NMC 13844, Pl. 23, fig. 3; text-fig. 9B) shows a series of growth lines on the dorsal shield, the first of which has a clear anterior notch for the pineal body (text-fig. 7B). The pineal body is further forward, however, and a further growth line curves round it indicating that the animal continued growing after the initiation of shield formation. The second growth line appears to mark the stage at which growth of the animal ceased; however, it is still inside the lateral dorsal canals and indicates that they had not been invested by the shield at this point.

From this evidence it appears that the Anchipteraspidae had developed the ability to continue growth once the shield had started to form but that the ability was still limited, comparable to the stage reached in the primitive pteraspidae *Protopteraspis* in which the shield fused shortly after investing the lateral dorsal canals of the sensory canal system.

EVOLUTIONARY RELATIONSHIPS OF THE PTERASPIDIDAE

Various authors have derived the Pteraspidae from a number of different heterostracan families. Tarlo (1962, 1967), Obrucsev (1967), and Halstead (1973) agreed in deriving the Pteraspidae from the Traquairaspidae, a view followed by Broad (1971) and more recently by Dineley and Loeffler (1976). Stensiö (1958) believed that the ancestors of the Pteraspidae were forms like the psammosteids in which belts of smaller scales separate the larger plates. Obrucsev (1945) believed that the Pteraspidae evolved from the Cyathaspididae and Denison (1964, 1973) followed this view.



TEXT-FIG. 9. Growth stages in heterostracan dorsal shields. A, *Pionaspis amplissima* (from Dineley and Loeffler 1976). B, *Ulutitaspis aquilonia*, NMC 13844. C, *Belgicaspis crouchi* (from White 1973). For explanation of abbreviations see text-fig. 2.

The discovery of the subfamily Anchipteraspidae provides new and stronger evidence in favour of the development of the Pteraspidae from the Cyathaspidae. Evidence from the arrangement of plates in the dorsal shield shows that evolutionary development was not totally by a process of fusion or of subdivision of dermal elements but by a combination of the two processes, thus supporting the views of Denison (1964) and Westoll (1967).

Denison (1964, pp. 465-466) set out the arguments in favour of the derivation of the Pteraspidae from the Cyathaspidae and this plan was also followed by Broad (1971) and Dineley and Loeffler (1976) in their argument for a derivation from the Traquairaspidae. I have used the same headings in the following assessment of the contribution of the Anchipteraspidae towards a solution of the problem.

1. The known geological record of the two groups was cited as favouring the derivation of the Pteraspidae from the Cyathaspidae by Denison (1964); however, Dineley and Loeffler (1976) showed that this was equally true for a derivation from the Traquairaspidae which range from the Wenlockian to the early Dittonian. Recent work on *Protopteraspis* from the Canadian arctic (Elliott and Dineley 1983) suggests that they are Pridolian in age in this area which may therefore be an evolutionary centre for the genus. In many localities they are preceded in the same stratigraphic sections by members of the Anchipteraspidae. The cyathaspid *Listraspis canadensis* which shows most similarity to the Anchipteraspidae and is probably the most closely related form is known only from British Columbia. It was dated as late Downtonian by Denison (1964); however, this date has been questioned by Dineley and Loeffler (1976) who do not feel so precise an estimate can be gained given the present level of knowledge on the cyathaspids and traquairaspids on which it is based.

2. Denison viewed the epitega, branchial plates, and ventral shield of the Cyathaspidae as comparable to the plates of the pteraspid shield; however, Dineley and Loeffler (1976) considered

that these were more closely comparable to plates in the traquairaspidid head shield. The Anchipteraspidinae appear to occupy an intermediate position in which the plates can be directly compared with those found in both the Cyathaspididae and the Pteraspididae.

In cyathaspidids the branchial plate is usually flat, elongated, and notched on the dorsal margin to form the branchial opening. It is also generally separate, though in *Listraspis* it is fused to the dorsal shield and in the Ctenaspidinae it has also been incorporated into the dorsal shield. The branchial plate of pteraspidids is fused to the dorsal shield, and even in the earliest representatives is enfolded to form a branchial duct. Though in the Anchipteraspidinae the plate is normally flat and fused to the dorsal shield, in *U. truncata* a branchial duct is formed by the partial enfolding of the branchial plate. This plate would require little change to form a branchial plate of pteraspidid type.

The orbito-cornual plates of the Anchipteraspidinae can also be directly compared with the separate orbital and cornual plates of the Pteraspididae and the orbital and lateral epitega of the Cyathaspididae. In the Anchipteraspidinae the plate is clearly demarcated into an orbital and a cornual part by an abrupt narrowing, and in the holotype of *Anchipteraspis crenulata* the ornamentation of the plate is disrupted at this point, possibly indicating the incipient development of separate plates. Denison (1964) has suggested that the cornual plates of pteraspidids were derived from a pair of scales attached to the posterolateral corners of the dorsal shield, a view apparently supported by the scale-like posterior cornual plates present in juvenile specimens of *Lampraspis tuberculata* (Denison 1973). However, the earliest members of the Pteraspidinae, the genus *Protopteraspis*, have in all cases well-developed cornual plates, and on functional grounds it also seems more likely that an outgrowth of the dorsal shield, initially developed as a control surface, would be retained and developed into separate plates. Such outgrowths have developed independently in the Cyathaspididae, *Listraspis* and *Ctenaspis* showing well-developed lateral laminae, and have been reported in the Traquairaspididae (Broad 1971).

Enclosed orbits are not a normal feature in the Cyathaspididae though they are present in the Ctenaspidinae and in *Listraspis*, a feature explained by Denison (1964) as being the result of fusion of a suborbital plate. Such plates have been described in articulated cyathaspidids by Kiaer (1932) and Dineley and Loeffler (1976). In *A. crenulata* disruption of the ornamentation below the orbit may be due to the incorporation of a suborbital plate or to the growth of the orbital plate down and around the orbit.

The pineal area in the advanced Cyathaspidinae probably remained naked longer than adjacent areas of the shield (Dineley and Loeffler 1976), thus the pineal plate of pteraspidids could have developed as a new centre of ossification in the postrostral field of cyathaspidids. *Listraspis* has a large pineal prominence and the members of the Anchipteraspidinae also have large pineal areas covered by separate plates.

The dorsal spine is a separate element in the Pteraspidinae and its development has been attributed (White 1935; Denison 1960, 1964) to the attachment of a dorsal ridge scale to the posterior margin of the dorsal disc and its gradual incorporation into the disc. The particularly scale-like dorsal spines of *Pteraspis rostrata* (White 1935) and *P. carmani* (Denison 1960) have been cited as evidence to support this view. Scale-like dorsal spines seem, however, to have been developed for functional reasons in flat-bodied forms, particularly protaspids, which may have been bottom dwellers and as such may not have required strongly functional keels. For this reason scale-like dorsal spines are seen as a later development in the Pteraspidinae, a view supported by the fact that the early members of the subfamily possess well-developed dorsal spines as do the Anchipteraspidinae.

In the Cyathaspididae a scale-like dorsal spine has been identified in *Ariaspis* (Denison 1964; Dineley and Loeffler 1976). In the specimen illustrated by Dineley and Loeffler the scale is less obviously demarcated from the rest of the shield and appears to be part of a band of scale-like elements forming the posterior margin of the dorsal shield. A similar band is present in a specimen of *Archegonaspis* cf. *A. schmidtii* illustrated by Loeffler and Jones (1976). If these elements are scales they appear to have been totally incorporated into the shield and there is no evidence to suggest that they would retain their identity within the shield to the extent of developing as separate plates.

The crest on the central epitegum in *Cyathaspis* has been described as a real dorsal spine

comparable with that of *Pteraspis* (Kiaer 1932). Similar crests are developed in *Ctenaspis* and *Listraspis* among the cyathaspidids, and erect dorsal spines are also present in two traquairaspidids described by Broad (1971). In none of these forms is there any indication that the spine was anything more than a development of the dorsal disc.

In the Anchipteraspidinae the dorsal spine is a discrete element, separated from the dorsal disc. In several specimens the anterior margin is obscured by the development of short, irregular ridges which may indicate that the process of total separation of the spine was not yet complete. This suggests that the first stage in the development of the pteraspidid dorsal spine was not the attachment of a scale to the posterior margin of the dorsal shield but the development of a posterior median crest, an adaptation of functional value to the animal. Once the crest had developed it would have separated to form a discrete element by the development of a new centre of growth and as part of the process of separate development of the epitegal areas taking place in the Cyathaspidinae at this time (Dineley and Loeffler 1976, pp. 104–107).

3. The microstructure of the shield of the Anchipteraspidinae is too poorly preserved to shed any light on the closeness of its relationship to the Cyathaspidinae and Pteraspidinae.

4. The lateral line canal system of Pteraspididae is easily derivable by minor modification of the simple pattern of cyathaspidids (Denison 1964, p. 465), though Broad (1971) and Dineley and Loeffler (1976) have suggested that this is more easily derived from that of certain traquairaspidids. In the Anchipteraspidinae the system is similar in all respects to that found in *Protopteraspis*; however, in *Anchipteraspis crenulata* the system still displays a rectangular appearance strongly reminiscent of the cyathaspidid type, normally an almost diagrammatically simple combination of longitudinal canals and transverse commissures. However, Kiaer and Heintz (1935) have noted an evolutionary trend towards a more regular and complete dorsal pattern in *Poraspis*. The anchipteraspidinid-pteraspidinid type of canal system could be developed from the basic cyathaspidid system by a process of fusion, and just such a system is found in *Ctenaspis*, a specialized cyathaspidid thought (Denison 1964) to have been derived from the Cyathaspidinae. In fact the resemblance is strong enough to have led Kiaer (1930) to suggest that the pteraspids were derived from *Ctenaspis*.

5. The dentine ridges of pteraspidids are typically narrow crested and crenulate. This type of ridge is also found in *Listraspis* and is characteristic of the Anchipteraspidinae. It is not considered that the traquairaspidid type of ornament could easily give rise to the pteraspidid ridge as suggested by Broad (1971).

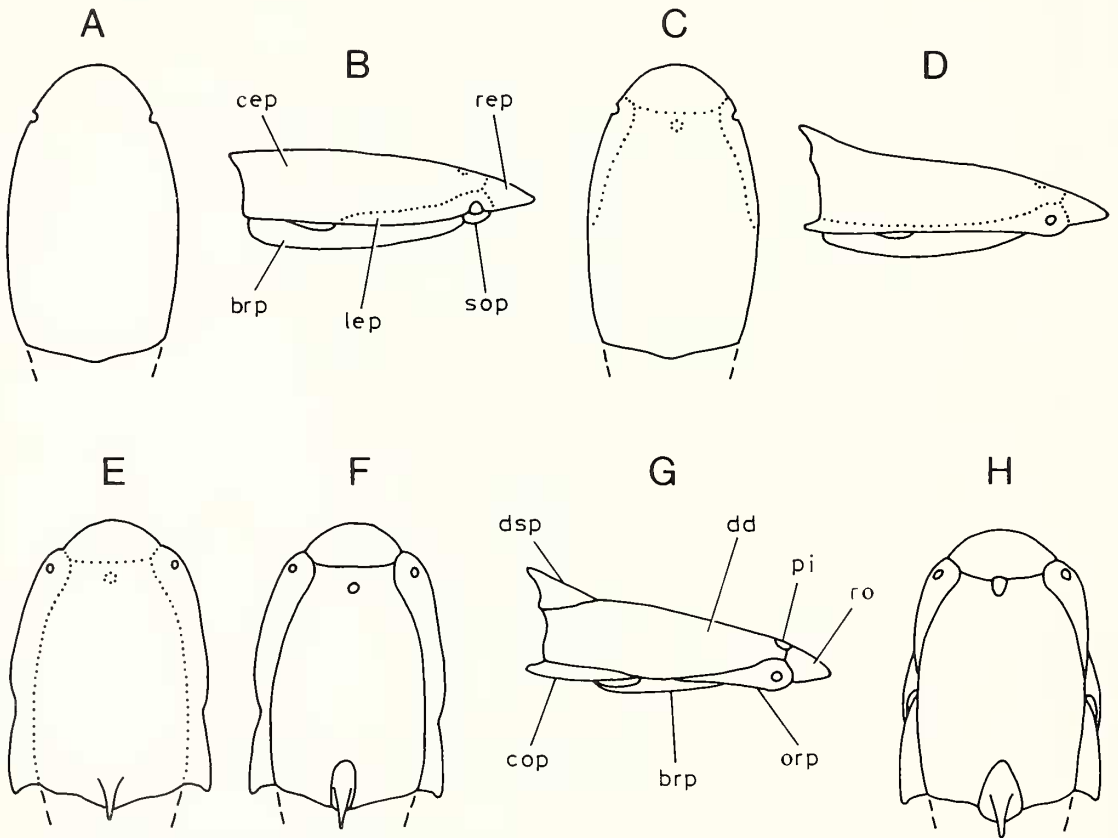
6. The narrow ornamented pre-oral surface typical of *Protopteraspis* is found in a primitive condition in the maxillary brim of *Listraspis* (Denison 1964) and other cyathaspidids. The Anchipteraspidinae also show this feature, *A. crenulata* bears only a narrow ornamented area but in *U. truncata* it is well developed. No feature of this type has been reported in the Traquairaspididae.

Interpretations of the relationships of the most well-known heterostracan groups, the Pteraspididae, Cyathaspididae, Psammosteida, and Traquairaspididae, has been dependent to a very great extent on views on the way in which the dermal shield developed. The Lepidomorial Theory of Ørvig (1951) though originally based on the development of elasmobranch scales was applied by Stensiö (1958) to growth in the Heterostraci and provided support for the evolutionary development of the shield by a process of fusion. This view was embodied in the evolutionary scheme of Halstead (1973), which begins with the fully tessellated *Eriptychius* and *Tesseraspis* and leads to two major groupings of heterostracans which progress from partially tessellate to non-tessellate forms. One group passes through the partially tessellated *Kallostrakon*, *Corvaspis*, and *Cardipeltis* to produce the non-tessellated Cyathaspididae and Amphiaspididae; the other progresses via *Weigeltaspis*, the Psammosteida, and the Traquairaspididae to produce the non-tessellate Pteraspididae. However, as noted by Janvier (1981), the recent discoveries of lower Ordovician remains (Ritchie and Gilbert-Tomlinson 1977), showing no indication of tesserae, make this scheme less than satisfactory, and the independent derivation of the Pteraspididae and Cyathaspididae is unlikely as the shape and distribution of the dermal plates in both groups is similar.

Halstead (1973) considers the psammosteids to be ancestral to the pteraspids; however, there is much stronger evidence to suggest that the reverse is true (Obruchev 1947, 1967; Westoll 1967). The

main plates of the early psammosteids are homologous with those of pteraspids, though an additional postorbital plate is present and the large plates are separated by a scale mosaic. This latter innovation may demonstrate a further advantage in growth, permitting a longer growth period in this family. Young stages of early forms such as *Drepanaspis* are very pteraspid in appearance (Gross 1963) and show most similarity to the dorsoventrally depressed early Devonian pteraspids such as *Protaspis* in which the cornuals are small and the branchial plates are large and have posterior branchial openings (Miles 1971). It was probably from among these forms that the drepanaspids were evolved.

It seems that more complex processes than simple fusion or subdivision may have been at work in the development of the shield (Obruchev 1943; Denison 1964; Westoll 1967) and evolutionary advancement within the Heterostraci should not be gauged automatically by the degree to which fusion of the shield has progressed.



TEXT-FIG. 10. Stages in the development of the heterostracan dorsal shield from the Cyathaspididae to the Pteraspidae. A, cyathaspidid with undivided dorsal shield and separate branchial plate. B, C, cyathaspidinid with dorsal shield divided into epitega. D, E, cyathaspidinid in which the lateral epitega are developed to form laminae, the orbit is enclosed, the branchial plate fused, and the dorsal spine developed as an outgrowth of the dorsal disc. F, anchipteraspidinid in which separate growth centres initiated in pineal and dorsal spine areas, and development of shield occurs before maturity. G, H, pteraspidinid in which peripheral growth of plates continues through ontogeny. For explanation of abbreviations see text-fig. 2.

CONCLUSIONS

It is proposed here that the Pteraspidae evolved from the Cyathaspididae during the Pridolian via the new subfamily Anchipteraspididae. This may have been a rapidly occurring event in a restricted area as there have been no other reports of forms attributable to the Anchipteraspididae though *Protopteraspis*, the earliest pteraspidid, has a wide distribution (Blicek 1981; Elliott and Dineley 1983).

The processes taking place in the dorsal shield are initially the development of rostral, dorsal, and lateral epitega in a cyathaspidid (text-fig. 10A–C). Growth would be initiated at maturity from separate growth centres in the epitega and fuse peripherally on contact, though the branchial plate would remain separate. *Pionaspis* is an example of this stage (Dineley and Loeffler 1976). Subsequently the lateral epitega would be developed to form lateral laminae and the orbit would be enclosed by the fusion of a sub-orbital plate (text-fig. 10D, E). The dorsal spine would be developed as an extension of the dorsal disc and fusion of the branchial plate would take place; however, growth of the shield would still be initiated at maturity. *L. canadensis* is an example of this stage (Denison 1964). The next stage is that reached in the Anchipteraspididae and requires merely the initiation of growth centres in the pineal area and at the dorsal spine, and the initiation of shield development before maturity to allow limited growth before the final fusion (text-fig. 10F). The final stage, embodied in *Protopteraspis*, requires shield growth to be initiated early allowing separate development of the plates by peripheral growth through ontogeny with fusion occurring at maturity (text-fig. 10G, H).

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REFERENCES

- BLIECK, A. 1981. Le genre *Protopteraspis* Leriche (Vertébrés Hétérostracés) du Dévonien inférieur Nord-Atlantique. *Palaeontographica*, **A173**, 141–159.
- BROAD, D. S. 1971. Upper Silurian and Lower Devonian Heterostraci from Yukon and Northwest Territories, Canada. Ph.D. thesis (unpublished), University of Bristol, 239 pp.
- 1973. Amphiaspidiformes (Heterostraci) from the Silurian of the Canadian arctic archipelago. *Bull. geol. Surv. Can.* **222**, 35–50.
- and DINELEY, D. L. 1973. *Torpedaspis*, a new Upper Silurian and Lower Devonian genus of Cyathaspididae (Ostracodermi) from arctic Canada. *Ibid.* 53–90.
- and LENZ, A. C. 1972. A new Upper Silurian species of *Vernonaspis* (Heterostraci) from Yukon Territory, Canada. *J. Paleont.* **46**, 415–420.
- DENISON, R. H. 1960. Fishes of the Devonian Holland Quarry Shale of Ohio. *Fieldiana, Geol.* **11** (10), 555–613.
- 1963. New Silurian Heterostraci from Southeastern Yukon. *Ibid.* **14** (7), 105–141.
- 1964. The Cyathaspididae: a family of Silurian and Devonian jawless vertebrates. *Ibid.* **13** (5), 309–473.
- 1970. Revised classification of Pteraspidae with description of new forms from Wyoming. *Ibid.* **20** (1), 1–41.
- 1973. Growth and wear of the shield in the Pteraspidae (Agnatha). *Palaeontographica*, **A143**, 1–10.
- DINELEY, D. L. 1964. New specimens of *Traquairaspis* from Canada. *Palaeontology*, **7**, 210–219.
- 1968. Osteostraci from Somerset Island. *Bull. geol. Surv. Can.* **165**, 49–63.
- 1976. The species of *Ctenaspis* (Ostracodermi) from the Devonian of Arctic Canada. In CHURCHER, C. S. (ed.), *Athlon: Essays on Palaeontology in Honour of Loris Shano Russell*.
- and LOEFFLER, E. J. 1976. Ostracoderm faunas of the Delorme and associated Siluro-Devonian Formations, Northwest Territories, Canada. *Spec. Pap. Palaeontology*, **18**, 218 pp.
- ELLIOTT, D. K. 1983. New Pteraspidae (Agnatha, Heterostraci) from the Lower Devonian of Northwest Territories, Canada. *J. Vert. Paleont.* **2** (4), 389–406.

- ELLIOTT, D. K. and DINELEY, D. L. 1983. New species of *Protopteraspis* (Agnatha, Heterostraci) from the Lower Devonian of Northwest Territories, Canada. *J. Paleont.* **56**, 2.
- FORTIER, Y. O. *et al.* 1963. Geology of the north central part of the Arctic archipelago, Northwest Territories (Operations Franklin). *Geol. Surv. Canada, Mem.* **320**, 117–129.
- GROSS, W. 1963. *Drepanaspis gemuendenensis* Schlüter. Neuuntersuchung. *Palaeontographica*, **A121**, 133–155.
- HALSTEAD, L. B. 1973. The Heterostracan fishes. *Biol. Rev.* **48**, 279–332.
- HEINTZ, A. 1973. Über die ältesten bekannten Wirbeltiere. *Naturwiss.* **26**, 49–58.
- JANVIER, P. 1981. The phylogeny of the Craniata with particular reference to the significance of fossil 'Agnathans'. *J. Vert. Paleont.* **1** (2), 121–159.
- JONES, B. and DIXON, O. A. 1977. Stratigraphy and sedimentology of upper Silurian rocks, northern Somerset Island, Arctic Canada. *Can. J. Earth Sci.* **14**, 1427–1452.
- KIAER, J. 1930. *Ctenaspis*, a new genus of Cyathaspidian fishes. *Skr. Svalbard Ishavet.* **33**, 1–7.
- 1932. The Downtonian and Dittonian vertebrates of Spitsbergen. IV. Suborder Cyathaspida. *Ibid.* **52**, 1–26.
- and HEINTZ, A. 1935. The Downtonian and Dittonian vertebrates of Spitsbergen. Suborder Cyathaspida. Part I. Family Poraspidae Kiaer. *Ibid.* **40**, 1–138.
- LOEFFLER, E. J. 1977. Additional late Silurian ostracoderms from the Leopold Formation of Somerset Island, Northwest Territories, Canada. *Palaeontology*, **20**, 661–674.
- and DINELEY, D. L. 1976. A new species of *Corvaspis* (Agnatha, Heterostraci) from the upper Silurian to lower or middle Devonian of the Northwest Territories, Canada. *Ibid.* **19**, 757–766.
- and JONES, B. 1976. An ostracoderm fauna from the Leopold Formation (Silurian to Devonian) of Somerset Island, Northwest Territories. *Ibid.* 1–15.
- MIALL, A. D. 1970. Continental marine transition in the Devonian of Prince of Wales Island, Northwest Territories. *Can. J. Earth Sci.* **7**, 125–144.
- and KERR, J. W. 1977. Phanerozoic stratigraphy and sedimentology of Somerset Island and northeastern Boothia Peninsula. *Geol. Surv. Can. Paper 77-1A*, 99–106.
- and GIBLING, M. R. 1978. The Somerset Island Formation: an Upper Silurian to ?Lower Devonian intertidal/supratidal succession, Boothia Uplift region, Arctic Canada. *Can. J. Earth Sci.* **15**, 81–189.
- MILES, R. S. 1971. *Palaeozoic fishes*. Chapman and Hall, London, 259 pp.
- MOY-THOMAS, J. A. 1939. *Ibid.* 1–149.
- OBRUICHEV, D. V. 1943. A new restoration of *Drepanaspis*. *C.r. Acad. Sci. USSR (Dokl. Akad. Nauk SSSR)*. **41**, 268–71.
- 1945. The evolution of the Agnatha. *Zool. zh.* **24**, 257–272. [In Russian.]
- 1947. Vertebrata. In *Atlas of the guide forms of the fossil faunas of the USSR*. Vol. 3. Devonian, 191–206.
- 1967. On the evolution of the Heterostraci. In LEHMAN, J. P. (ed.). *Colloques. int. Cent. natn. Rech. scient.* **104**, 13–29.
- ØRVIG, I. 1951. Histologic studies of Placoderms and fossil Elasmobranchs. 1. The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. *Ark. Zool.* **2**, 321–454.
- RITCHIE, A. and GILBERT-TOMLINSON, J. 1977. First Ordovician vertebrates from the Southern Hemisphere. *Alcheringa*, **1**, 351–368.
- STENSIÖ, E. A. 1958. Les cyclostomes fossiles ou Ostracodermes. In GRASSÉ, P. P. (ed.). *Traité de Zoologie*, **13** (i), 173–425. Paris.
- TARLO, L. B. 1962. The classification and evolution of the Heterostraci. *Acta palaeont. pol.* **7**, 249–290.
- 1967. The tessellated pattern of dermal armour in the Heterostraci. *J. Linn Soc. (Zool.)*, **47**, 45–54.
- THORSTEINSSON, R. 1967. Preliminary note on Silurian and Devonian ostracoderms from Cornwallis and Somerset Islands, Canadian Arctic Archipelago. *Colloques int. Cent. natn. Rech. scient.* **163**, 45–47.
- 1980. Stratigraphy and Conodonts of Upper Silurian and Lower Devonian rocks in the Environs of the Boothia Uplift, Canadian Arctic Archipelago. Part I. Contributions to Stratigraphy. *Bull. geol. Surv. Can.* **292**, 1–38.
- and TOZER, W. 1963. Geology of northern Prince of Wales Island and northwestern Somerset Island. In FORTIER, Y. *et al.* Geology of the north central part of the Arctic archipelago, Northwest Territories (Operation Franklin) *Mem. geol. Surv. Canada*, **320**, 117–129.
- TOOMBS, H. A. and RIXON, A. E. 1950. The use of plastics in the 'Transfer Method' of preparing fossils. *Museums J.* **50**, 105–107.
- UYENO, T. T. 1980. Stratigraphy and Conodonts of Upper Silurian and Lower Devonian rocks in the Environs of the Boothia Uplift, Canadian Arctic Archipelago. Part II. Systematic Study of Conodonts. *Bull. geol. Surv. Can.* **292**, 39–75.

- WESTOLL, T. S. 1967. *Radotina* and other tesserate fishes. *J. Linn. Soc. (Zool.)*, **47**, 83–98.
- WHITE, E. L. 1935. The Ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. *Phil. Trans. R. Soc.* **B225**, 381–457.
- 1950. Vertebrate faunas of the Lower Old Red Sandstone of the Welsh Borders. *Bull. Brit. Mus. (Nat. Hist.) Geol.* **1**, 51–67.
- 1958. Original environment of the Craniates. In WESTOLL, T. S. (ed.). *Studies on fossil vertebrates*. Athlone Press, London, 212–233.
- 1973. Form and growth in *Belgicaspis* (Heterostraci). *Palaeontographica*, **A143**, 11–24.
- ZYCH, W. 1931. *Fauna ryb Devonii i Downtoni Podola*. Lwów, 91 pp.

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